Electrofishing and Its Harmful Effects on Fish

Information and Technology Report
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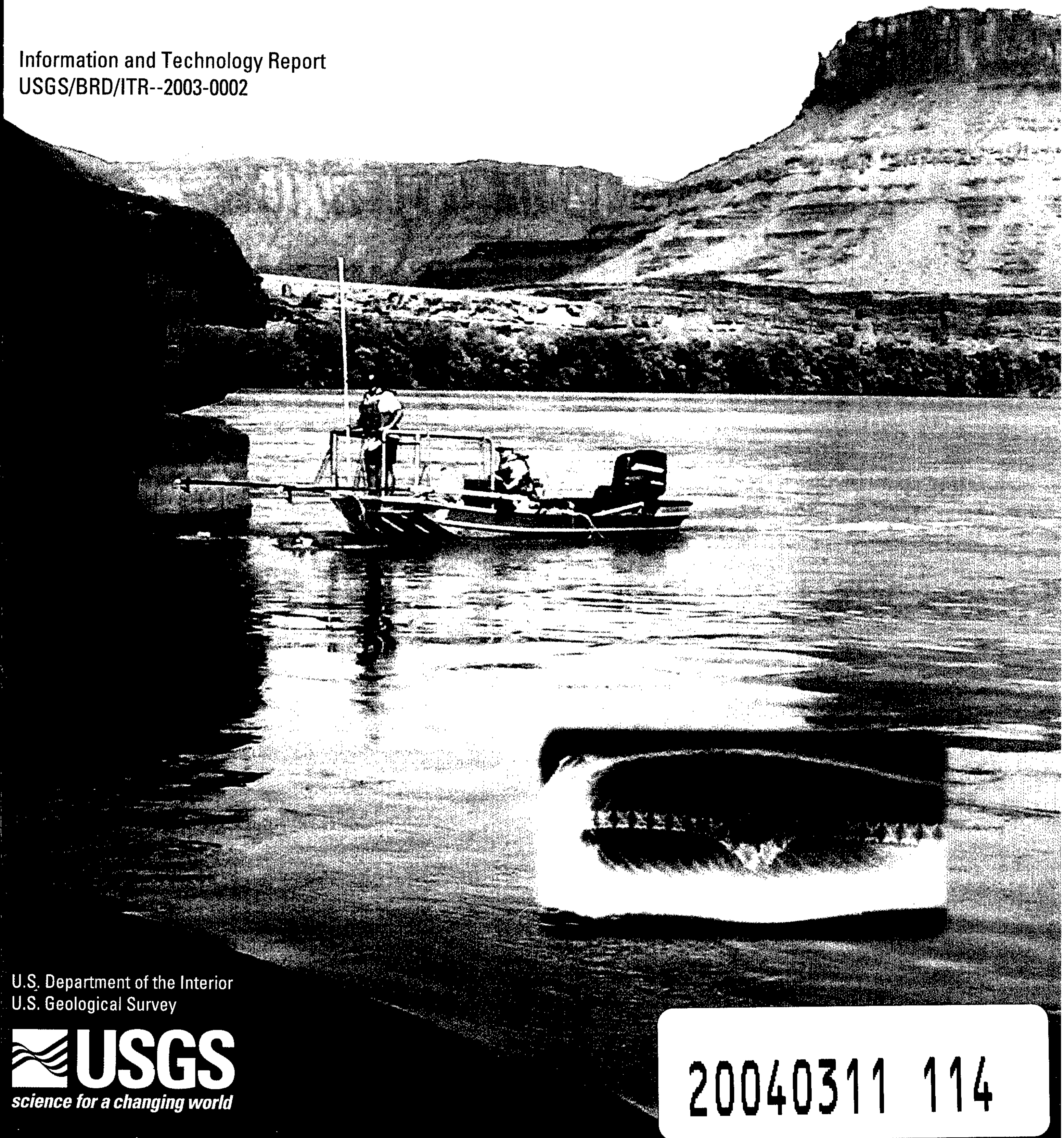

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The cover photograph was taken on the Colorado River a few miles below Potash, Utah, on June 9, 2003; it was provided by, and is used with permission of, Doug Osmundson, U.S. Fish and Wildlife Service, Colorado River Fishery Project, Grand Junction, Colorado. Agencies electrofishing in the Colorado River Basin have instituted measures to minimize harmful effects on fish, including injuries such as the extreme example illustrated in the inset X-ray. That dorsal-view X-ray of spinal misalignment and fractured vertebrae in an electrofished rainbow trout (*Oncorhynchus mykiss*) was provided in 1991 by, and is used with permission of, Norman G. Sharber, Flagstaff, Arizona.

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Electrofishing, which involves a very dynamic and complex mix of physics, physiology, and behavior, has been a valuable sampling technique for over half a century, but its potentially harmful effects on fish must be recognized, monitored, and avoided or minimized, especially with respect to populations of endangered species. Spinal injuries and associated hemorrhages, although often not externally obvious or fatal, can occur anywhere in the electrofishing field at or above the intensity threshold for twitch. These injuries are believed to result from powerful convulsions of body musculature caused mostly by sudden changes in voltage. Significantly fewer spinal injuries are reported when direct current, low-frequency pulsed direct current (#30 Hz), or specially designed pulse trains are used. Salmoninae are especially susceptible. Endangered cyprinids of the Colorado River Basin are generally much less susceptible, but the endangered catostomid *Xyrauchen texanus* appears sufficiently susceptible to warrant minimal-use policy. Other harmful effects, including bleeding at gills or vent and excessive physiological stress, are also of concern. Mortality, usually by asphyxiation, is a common result of excessive exposure to tetanizing intensities near electrodes or poor handling of captured specimens. Reported effects on reproduction are contradictory, but electrofishing over spawning grounds can harm embryos.

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Electrofishing and Its Harmful Effects on Fish

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Foreword

This report provides a comprehensive synthesis of the literature related to electrofishing with an emphasis on adverse effects to fish. The sections on "Electric Fields in Water," "Responses of Fish to Electric Fields," "Harmful Effects of Electrofishing on Fish," "Factors Affecting Electrofishing Injury and Mortality," and "Conclusions" are especially valuable to all field biologists who use electrofishing as a sampling tool. This information provides insight on how to effectively use this valuable sampling tool while minimizing adverse effects to fish. The recommentation of experimental testing is especially important when electrofishing is to be used to sample threatened or endangered fishes so that necessary precautions can be taken to avoid injury or mortality. This thorough overview provides a valuable reference to biologists, managers, and students for understanding: (1) the principles of electrofishing; (2) concepts of electrical transmission in water and fish; and (3) ways to reduce fish injury and mortality. Application of this knowledge will ensure that studies are designed to minimize biased results and adverse impacts.

Dr. Richard S. Wydoski, Editor

Preface

In 1990, the Lower and Upper Colorado River regions of the U.S. Bureau of Reclamation planned a three-phased study to identify and address the potential harmful effects of electrofishing on endangered fish in the Colorado River Basin. Phase I consisted of a comprehensive literature review and synthesis of existing information on effects of electrofishing with recommendations for future research and interim guidelines to minimize harmful effects (Snyder, 1992a, original version of this report). Phase II consists of controlled laboratory and field experiments to address selected questions and concerns remaining after Phase I. Phase III will field test the effectiveness of promising techniques or protocols suggested as a result of Phases I and II. Portions of the 1992 Phase I report have been abstracted for articles to provide a brief overview of the problem (Snyder, 1992b, 1995) and specifically discuss known effects on fish reproduction, embryos, and larvae (Snyder, 1993, 1994). Investigations concluded thus far under Phase II include those by Cowdell and Valdez (1994), Ruppert and Muth (1995, 1997), Ruppert (1996), Muth and Ruppert (1996, 1997), and Meismer (1999); another is nearing completion (Hawkins, personal communication).

This Final Report of Colorado State University Larval Fish Laboratory to the U.S. Bureau of Reclamation Upper Colorado Regional Office (Salt Lake City, Utah) updates the Phase I (Snyder, 1992a) review and synthesis of electrofishing literature based on over 60 additional technical papers, reports, and newsletter and magazine articles published on electrofishing and its effects between 1992 and 2000. It also updates recommendations for interim guidelines on use of electrofishing for collection of endangered fishes in the Colorado River Basin and for future research. As a recognized, peer-reviewed publication, through and in cooperation with the U.S. Geological Survey, it is more citable in future technical publications and available to a much wider audience.

Contents

Contents (continued)

Tables

Figures

Contents (concluded)

Figures (concluded)

Appendices

Electrofishing and Its Harmful Effects on Fish

By

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Abstract. Electrofishing, a valuable sampling technique in North America for over half a century, involves a very dynamic and complex mix of physics, physiology, and behavior that remains poorly understood. New hypotheses have been advanced regarding "power transfer" to fish and the epileptic nature of their responses to electric fields, but these too need to be more fully explored and validated.

Fishery researchers and managers in the Colorado River Basin, and elsewhere, are particularly concerned about the harmful effects of electrofishing on fish, especially endangered species. Although often not externally obvious or fatal, spinal injuries and associated hemorrhages sometimes have been documented in over 50% of fish examined internally. Such injuries can occur anywhere in the electrofishing field at or above the intensity threshold for twitch. These injuries are believed to result from powerful convulsions of body musculature (possibly epileptic seizures) caused mostly by sudden changes in voltage as when electricity is pulsed or switched on or off. Significantly fewer spinal injuries are reported when direct current, low-frequency pulsed direct current (≤30 Hz), or specially designed pulse trains are used. Salmoniae are especially susceptible. Endangered cyprinids of the Colorado River Basin are generally much less susceptible, enough so to allow cautious use of less harmful currents for most recovery monitoring and research. However, the endangered catostomid *Xyrauchen texanus* appears sufficiently susceptible to warrant a continued minimal-use policy.

Other harmful effects, such as bleeding at gills or vent and excessive physiological stress, are also of concern. Mortality, usually by asphyxiation, is a common result of excessive exposure to tetanizing intensities near electrodes or poor handling of captured specimens. Reported effects on reproduction are contradictory, but electrofishing over spawning grounds can harm embryos. Electrofishing is often considered the most effective and benign technique for capturing moderate- to large-size fish, but when adverse effects are problematic and cannot be sufficiently reduced, its use should be severely restricted.

Key Words: Behavior, electric fields, electrofishing, epilepsy, fish, injuries, mortality, power transfer, responses, stress.

Introduction

Electrofishing, the use of electric fields in water to capture or control fish, has been a valuable sampling technique in North America for over half a century, but there has been increasing concern among fishery biologists and managers regarding its potential for harming fish. Much of this increased concern began when Sharber and Carothers (1988) documented substantial injury to the spinal column and associated tissues of 44 to 67% of large rainbow trout (over 300 mm TL) collected with pulsed direct current (PDC) from the Colorado River in Glen Canyon National Recreation Area and Grand Canyon National Park. Most of the injuries were detected only by X-ray analysis or necropsy in fish that appeared externally normal (Fig. 1). This report quickly prompted similar investigations elsewhere which also resulted in reports of substantial numbers of PDC-caused spinal injuries in rainbow trout (up to 98%), as well as brook trout, brown trout, cutthroat trout, Arctic graying, river carpsucker, northern pike, and walleye (Holmes, 1990;

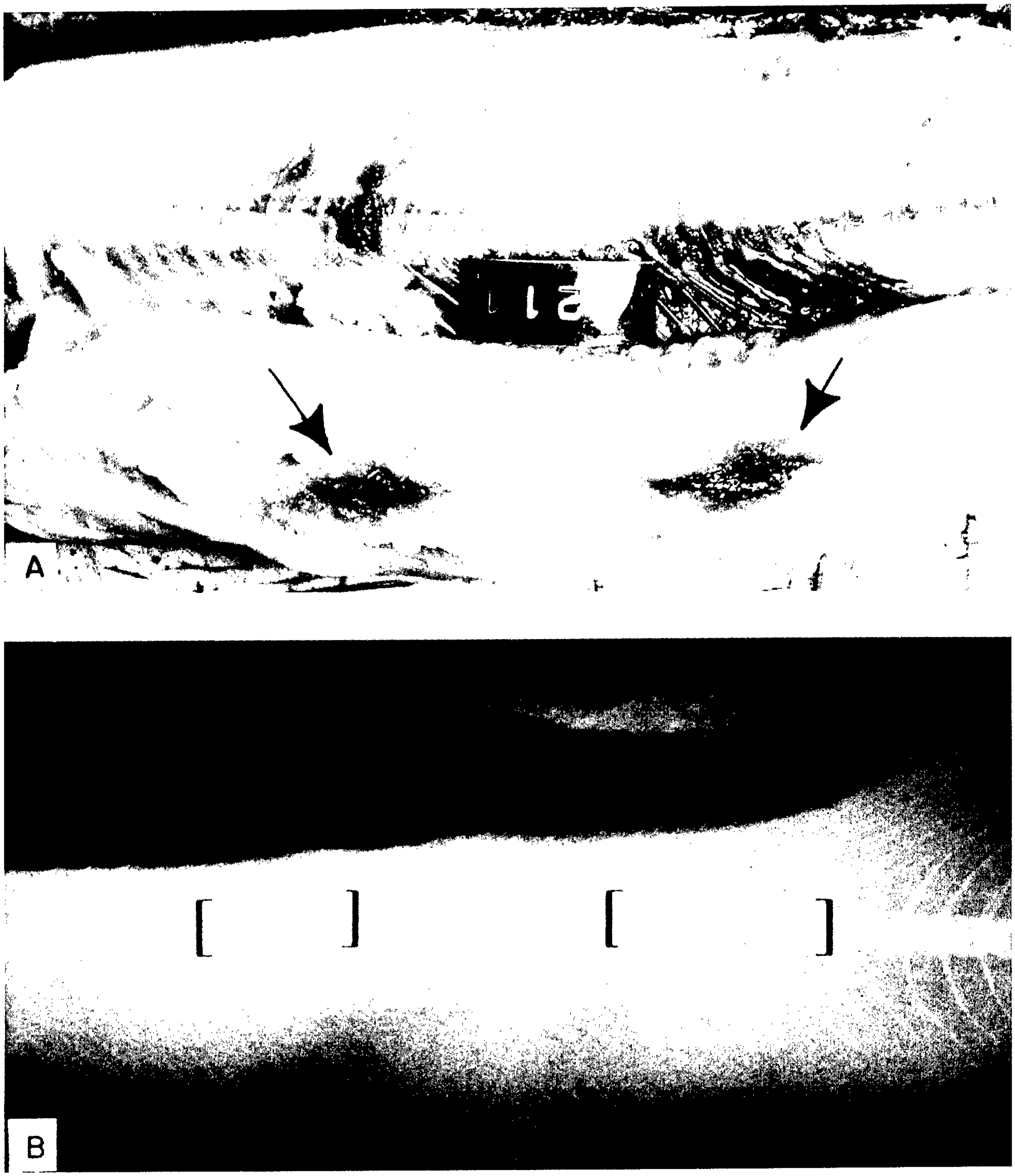

Fig. 1. Electrofishing-induced injuries to the spinal column and associated hemorrhages in rainbow trout (*Oncorhynchus mykiss*). (Photograph A is both sides of a fillet exposing injuries. Photograph B is a lateral-view X-ray of the same injuries prior to necropsy. Reproduced with permission from Fig. 2 in Sharber and Carothers, 1988.)

Meyer and Miller, 1990; Wyoming Game and Fish Department, 1991; Fredenberg, 1992; Hollender and Carline, 1992, 1994; Newman, 1992; Roach, 1992; Taube, 1992; McMichael, 1993; Zeigenfuss, 1995; Dalbey et al., 1996; Grisak, 1996; Thompson et al., 1997a).

The results of Sharber and Carothers' (1988) study also alarmed regional biologists and managers of the National Park Service and U.S. Bureau of Reclamation about continued use of electrofishing to monitor endangered humpback chub in the Grand Canyon. In a memorandum to the Glen Canyon Ecological Studies program manager (12 July 1990), the superintendent of Grand Canyon National Park, J.H. Davis, suggested that until concerns over potential adverse effects could be resolved, electrofishing in Glen Canyon National Recreation Area and Grand Canyon National Park should be kept to a minimum and be used in such a way as to minimize possible stress and injury to humpback chub. Concern also increased about the use of electrofishing to study endangered Colorado pikeminnow, humpback chub, bonytail, and razorback sucker in the Upper Colorado River Basin. As a result, the U.S. Bureau of Reclamation sponsored the three-phase study described in the Preface of this report.

The objectives of the original Phase I report (Snyder, 1992a) and this update were to: (1) review and synthesize the literature on electrofishing including the nature of electric fields in water, responses of fish to those fields, its harmful effects on fish, and the factors (specific aspects of electrofishing fields and fish) potentially affecting injury and mortality in fish; (2) answer specific questions regarding the use of electrofishing to capture threatened, endangered, and native fishes in the Colorado River Basin; and (3) provide recommendations for interim policy and future research to avoid or minimize the harmful effects of electrofishing on those fishes. Although specifically intended to facilitate evaluation of current electrofishing policies by Colorado River Basin agencies, the review and synthesis is broad in scope and should be useful wherever the impacts of electrofishing are a concern. As author, I have brought little practical electrofishing experience to this project but also no prior biases or vested interests.

Methods

Publications up to year 2000 on electrofishing and particularly its effects on fish were identified primarily through electrofishing bibliographies (especially Burridge et al., 1990), electronic databases of literature (e.g., Fish and Fisheries Worldwide, Aquatic Science and Fisheries Abstracts, Biological Abstracts, Fish and Wildlife Reference Service, and Uncover), and the Literature Cited sections of published papers. Copies of most English-language and translated literature and many foreign-language papers were obtained, scanned for content, and, if pertinent, reviewed for inclusion in this report. Literature identified for the earlier version of this report (Snyder, 1992a) was catalogued with keywords and content codes in a bibliographic database (Reference Manager, Institute for Scientific Information, Philadelphia, Pennsylvania). An indexed bibliography was generated from this database (Snyder and Johnson, 1991) and appended to the original report (Snyder, 1992a). Both that bibliography and Burridge et al. (1990) were expanded upon and updated by Miskimmin and Paul (1997a).

Information derived from published literature and limited-distribution reports was supplemented by data, observations, theories, and recommendations in unpublished manuscripts and anecdotal personal communications.[1] Contributions regarding unpublished and ongoing work, as well as personal observations, experiences, and suggestions, were solicited through a request printed in the American Fisheries Society magazine Fisheries, vol. 16, no. 3, p. 52, May–June 1991) and several other fishery-related bulletins and newsletters. Approximately 30 responses were received. Several recognized authorities and electrofishing gear manufacturers also shared their knowledge, views, and unpublished manuscripts. Some contacts were made and information exchanged during special sessions on electrofishing injuries that were held as part of annual meetings of the Western Division of the American Fisheries Society in 1991 (Bozeman, Montana) and 1992 (Fort Collins, Colorado). Finally, a questionnaire was prepared to solicit local observations and recommendations on electrofishing (Appendix II in Snyder, 1992a). The survey forms were distributed to researchers working in the Colorado River Basin and to faculty and students in fishery biology at Colorado State University.

Scientific names and families of fishes referenced by common names herein are given in Appendix A and follow Robins et al. (1991a,b). When known, fish lengths are specified as total length (TL), fork length (FL) or standard length (SL), conductivity as ambient or standardized to 25° C, and electrical output and field intensities as mean ($_m$), root-mean-square ($_{rms}$), or peak ($_p$). In many cases these important distinctions were not reported. Except when directly pertinent to the text, readers are referred to Appendix B for environmental and electrical parameters associated with electrofishing investigations discussed herein.

[1]Unpublished manuscripts and personal communications are fully identified on page 125 after "Literature Cited."

Results — Historical Overview

Electricity has been used by humans to kill, anesthetize, capture, drive, draw, tickle (arouse), guide, or screen (block, repel) fish since the mid 1800's (Vibert, 1967b; Halsband and Halsband, 1975, 1984; Hartley, 1990). Fishery researchers and managers often rely on electrofishing as their principal capture method for researching, monitoring, and managing stocks of freshwater fishes, especially salmonids (e.g., Weber, 1997). In 1863, a British patent was granted to Isham Baggs for electric fishing, but widespread development and use of the technique did not occur until the 1950's (Hartley, 1990; Reynolds, 1995). Halsband and Halsband (1975, 1984) provided a particularly detailed history of research on fish in electric fields, especially with regard to German contributions. However, man's technological developments are often modifications or imitations of nature's own. Before the evolution of modern man, certain species of fish developed powerful electric organs which were probably used much like their modern descendants to detect and capture prey or ward off predators (Marshall, 1966; Hyatt, 1979). The stunning or narcotizing effects of electric fishes were known and used for medical purposes by the ancient Greeks, and study of electric fishes during the 18th and 19th centuries was instrumental in our understanding of the electrogenic nature of nerves and muscles (Wu, 1984).

Most of our knowledge of electrofishing practice, theory, and effects on aquatic organisms is well represented in three English-language European symposia publications edited by Vibert (1967a, from 1966 FAO symposium, United Nations Food and Agriculture Organization, Belgium), Cowx (1990, from 1988 EIFAC symposium, European Inland Fisheries Advisory Council, England), and Cowx and Lamarque (1990—also from 1988 EIFAC symposium); a German text by Halsband and Halsband (1975, English translation 1984); a Russian reference book by Sternin et al. (1972, English translation 1976); and a manual for a course on electrofishing offered nationwide through the National Conservation Training Center (formerly Fisheries Academy) of the U.S. Fish and Wildlife Service (latest version, Kolz et al., 1998). A book by Meyer-Waarden and Halsband (1975, German) and a symposium publication edited by Maiselis (1975, Russian with English summaries) also should be included in the list, but English translations are not available. Fishing with Electricity, edited by Cowx and Lamarque (1990), can serve as a relatively up-to-date academic text and basic reference, but not all of the information therein should be treated as fact; there are too many uncertainties and gaps in knowledge. Although this book is treated by distributors as a replacement for Vibert's (1967a) Fishing with Electricity, Vibert's book includes much information not in the new book. Halsband and Halsband (1975, 1984) is also a fine text on electrofishing, but it is based largely on German perspectives, experience, and research, and like Vibert (1967a), it is somewhat dated. Sternin et al. (1972, 1976) includes marine applications and is a very detailed treatise on the theory and practice of electrofishing based on Soviet research and summaries of world literature. Its Appendices 4 and 5 are tabulated summaries of fish response thresholds (without source references) and aftereffects on fish (reproduced in Snyder 1992a as Appendices III and IV, respectively). The manual for the U.S. Fish and Wildlife Service classroom and correspondence course on Principles and Techniques of Electrofishing (Kolz et al., 1998) is a loose-leaf, periodically updated volume in semi-outline format with a CD-ROM disk of supplemental simulations and exercises. Except for the article by Sharber and Carothers (1990) in Cowx (1990), a four-page synopsis in the article by Lamarque (1990) in Cowx and Lamarque (1990), and a few pages in Sternin et al. (1972, 1976), Halsband and Halsband (1975, 1984), and Kolz et al. (1998), the matter of electrofishing injury and mortality was not discussed extensively in any of these books or manuals.

Recognized authorities on electrofishing have long emphasized its benign qualities. For example, Halsband (1967) stated that "the harmlessness of electric current to fish and their food organisms has already been proved on several occasions." And in the foreword to their book, Sternin et al. (1972, 1976) suggested that the theory and practice of electrofishing in recent decades had put to rest concerns about deleterious effects on normal activity and natural reproduction in fish. More emphatically, Halsband and Halsband (1975, 1984) stated that "today we are convinced that electrical collecting, repelling, and stunning methods neither cause pain to animals nor injure them internally or externally, (apart from unavoidable exceptions)." However, these conclusions were premature because we now have considerable evidence that electrofishing injuries may have been more common than they appeared or were reported.

Spinal injuries in particular were not widely recognized because most are not externally obvious and can only be detected by X-ray analysis or necropsy. When present, even brands (temporary dark markings on the body; Fig. 2) were seldom associated, as they frequently are now, with at least moderately severe spinal injuries or hemorrhages. If captured fish had no notable external injuries, aside from occasional brands, and appeared to recover sufficiently to swim away, they were typically considered "unharmed" and expected to continue to behave, grow, and reproduce normally. As a result, electrofishing had often been considered not only the most efficient but the least-damaging collection technique available.

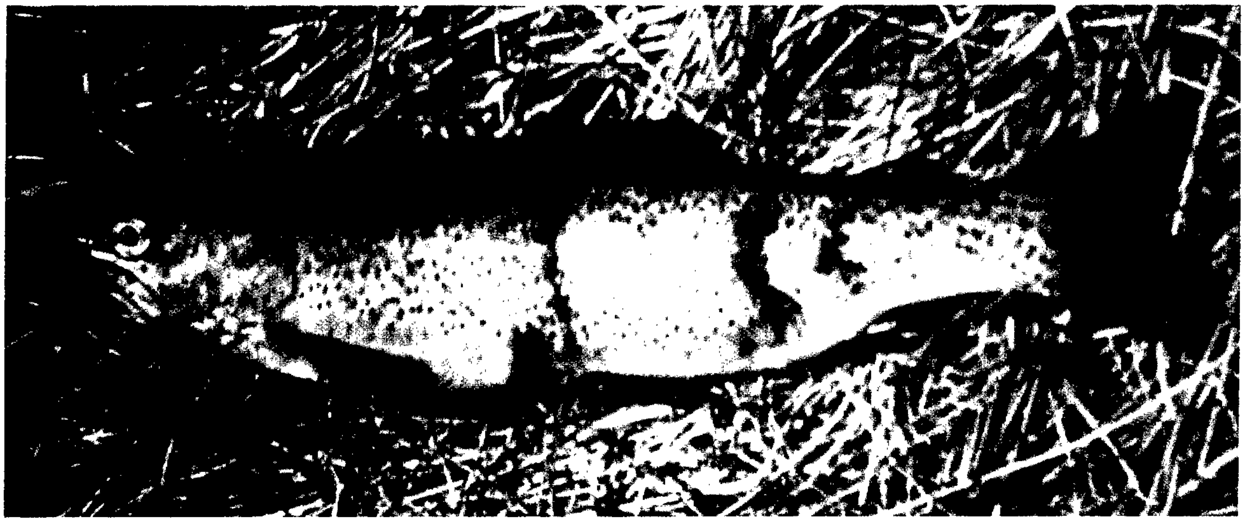

Fig. 2. Brands (bruises or dark pigmental discolorations) in rainbow trout (*Oncorhynchus mykiss*) caused by electrofishing. (Brands are usually temporary external manifestations of spinal injury, but injured fish often lack brands. Photograph provided by and reproduced with permission of W.A. Fredenberg, Montana Department of Fish, Wildlife, and Parks.)

Since Sharber and Carothers' (1988, 1990) report of substantial numbers of spinal injuries among electrofished rainbow trout, some agencies have begun to verify and further investigate the extent, conditions, and causes of electrofishing-induced spinal injuries (e.g., Holmes et al., 1990; Wyoming Game and Fish Department, 1990, 1991; Fredenberg, 1992; Sharber et al., 1994; others cited in the introduction). As a result, one agency, the Alaska Department of Fish and Game, imposed a moratorium on electrofishing in waters containing large rainbow trout (Holmes et al., 1990). Similarly, the Montana Department of Fish, Wildlife, and Parks (1994) issued regulations designed to limit injuries to fish, including restricted use of PDC over 30 Hz, and federal biologists in Idaho were discouraged from using any electrofishing techniques for capture of bull trout (Schill and Beland, 1995).

Many biologists across the continent and abroad now acknowledge that potential incidence of electrofishing injuries in otherwise normal-appearing specimens might be a serious concern, at least for some environmental conditions, equipment, and species. They have been asking: what species and size groups are affected, to what degree are they affected, what equipment, electrical parameters, and techniques are responsible, what specific mechanisms are involved, and what can be done to eliminate or minimize the problems?

Most of these questions are not new. Spinal injury has been associated with AC fields for over half a century (e.g., Hauck, 1949), but until the late 1980's, it had been largely overlooked as a significant problem with at least some forms of PDC. This perception endured despite only limited documentation of injuries caused by AC and some early publications documenting high incidence of injury with PDC (e.g., Horak and Klein, 1967).

Despite electrofishing's prominent role in fishery research and management, well-designed investigations to address many of these questions and to understand the general reactions of fish in electric fields are relatively few, often very limited in scope (frequently a by-product of another investigation), and difficult to compare because of differing objectives, gear, techniques, environmental conditions, species, and terminology. With regard to terminology, many researchers and authors fail to make critical distinctions between PDC and continuous, nonpulsed, direct current (DC), peak and mean output voltages or field-intensity values, or narcosis and tetany. Also, many reports of adverse effects are anecdotal or lack critical data on the circumstances of the observations or experiments. Perhaps as a result of these limitations, inconsistencies, and deficiencies, reported results sometimes seem so contradictory that they appear to follow the law of physics which states that for every action (report) there is an equal and opposite reaction (counter report).

Broader questions also continue to be considered. Biologists are concerned about potential effects of electrofishing on the survival, growth, reproduction, and general well-being of populations and communities. Horak and Klein (1967), Spencer (1967a), Hudy (1985), and Schneider (1992) reported that electrofishing injuries often heal and are not necessarily lethal or debilitating to fish. Although most fish apparently survive electrofishing-induced spinal injuries, Lamarque (1990) stated that growth certainly would be impaired. Sharber

and Carothers (1988, 1990) noted that we do not know how long fish with electrofishing injuries will survive and suggested that, at least for large rainbow trout (the subjects of their investigation), such spinal injuries might bias age, growth, and population studies based on mark-recapture techniques. Sharber and Carothers (1988, 1990) also cautioned that the detrimental impact of such injuries might be very significant for populations of fishes that are already low or endangered.

In an article abstracted from the 1992 version of this report (Snyder, 1995), I concluded that in situations where electrofishing injuries are a significant problem and cannot be adequately reduced (through gear, current, or procedural changes), use of the technique must be abandoned or severely limited. During the next couple of years, the message regarding potential harm to fish by electrofishing was relayed to the public by related articles in various newspapers and fishing and outdoor magazines (e.g., Holt, 1995; Ritchie, 1995; Cofer, 1996; Meyer, 1997). In direct response to my article, Schill and Beland (1995) expressed a grave concern that fishery biologists may be forced by public perception of the problem (Weber, 1997) to unduly give up or restrict use of one of the profession's most effective sampling tools. In particular, they observed that scientific discussion had "focused on small pieces of the puzzle" and had "largely ignored the more important question of population significance." They explained, by hypothetical example, that in most cases only very small portions of populations are sampled and even if incidences of injury and long-term mortality were very high (e.g., 50% and 25%, respectively), they would affect no more than one or two percent of the population as a whole. Furthermore, they continued, annual natural mortality for some species (e.g., stream salmonids in northern states) is so high that the long-term population effects of even greater electrofishing impacts could be further discounted. Schill and Beland (1995) also noted that biologists routinely sample lacustrine fish with gill nets and accept even 100% mortality because only a very small segment of the population is sacrificed. In some situations, captured fish are purposely sacrificed for subsequent analysis. Similar concerns over public perception of the problem were expressed by Wiley (1996) after Holt (1995) told "the truth about electrofishing." However, Cofer (1996), in revealing "the shocking truth," suggested that my article (Snyder, 1995) succeeded in stirring debate over often-overlooked side effects and that "in confronting the issue, scientists may have solved half the problem by recognizing that electrofishing—in its current form—is not always so benign."

Consistent with Schill and Beland's (1995) suggestion of insignificant adverse effects by electrofishing on populations, biologists such as Nehring (1991) and Schneider (1992) have documented that years of electrofishing, even with AC (Schneider, 1992), had not detrimentally affected the specific populations they monitored or managed. However, adverse effects that may be insignificant for large, widely distributed populations, might pose a significant additional threat to the survival or recovery of much smaller, localized populations of rare, threatened, or endangered species.

If electrofishing injuries occur in notable numbers of fish but do not significantly affect their population size (long-term survival, reproduction, recruitment) or health (growth, condition), perhaps the only real concerns in such situations are resource quality and public perception thereof. In some fish, spinal injuries result in permanently bent backs (Fig. 3) or related deformities (Fig. 4) which sometimes do not become obvious until well after exposure to the electric field. In other fish, spinal injuries might only be revealed by X-rays or dissection, possibly on an angler's dinner table.

The extent of concern about potential electrofishing injuries in North America has been exemplified by the formation of an informal working group on electrofishing injuries within the Western Division of the American Fisheries Society, special sessions on the matter held during annual meetings of the Western Division in July 1991 (Bozeman, Montana) and 1992 (Fort Collins, Colorado), and the attempted establishment of an Electrofishing Injury Network through the American Fisheries Society Fisheries Management Section. In Europe, a workshop on the harmful effects of electrofishing was organized by the EIFAC Working Group on Electric Fishing and held on 21 and 22 May 1992 in conjunction with the 17th Session of EIFAC in Lugano, Switzerland. Until the concerns are effectively resolved, the harmful effects of electrofishing are likely to be the subject of still more special sessions, workshops, and organizations.

Some state and provincial agencies have reviewed their concerns about deleterious effects of electrofishing and established policies, regulations, or guidelines for use of such techniques. Emphasizing available information on 15 species of regional interest, Miskimmin and Paul (1997a,b) and Paul and Miskimmin (1997) prepared a three-part report similar to this review for consideration by the Fisheries Management Division of Alberta Environmental Protection whose 1995 policy to minimize adverse effects of electrofishing on fish was being appealed. In the third part of that report, Miskimmin and Paul (1997b) reviewed and compared existing policies or guidelines from Canadian and U.S. jurisdictions. They acknowledged Montana as a leader in establishing a relatively strict state-wide policy and comprehensive standards to minimize electrofishing injury to aquatic life (Montana Department of Fish, Wildlife and Parks, 1994). Alberta's 1995 policy was similar to Montana's. Ontario and Washington also have official policies or guidelines

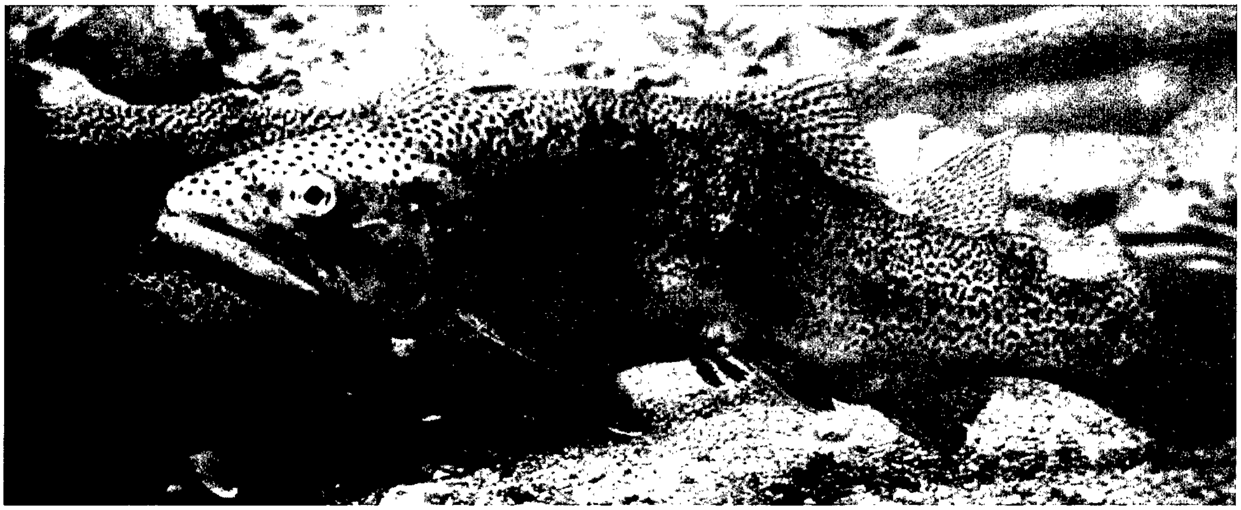

Fig. 3. Bent back in rainbow trout (*Oncorhynchus mykiss*) caused by electrofishing. (Photograph provided by and reproduced with permission of M.S. Quinton via W.A. Fredenberg, Montana Department of Fish, Wildlife, and Parks.)

intended to minimize injuries (established in 1986 and 1997, respectively), and Michigan was revising its electrofishing policy to include a section to the same end. Alaska, Idaho, Minnesota, New York, and Wyoming have unofficial policies or guidelines to minimize electrofishing injuries. With regard to electrofishing in waters inhabited by threatened or endangered species, Miskimmin and Paul (1997b) reported that the U.S. Fish and Wildlife Service allows use of only DC or PDC, prohibits spiked waveforms, and requires records of pertinent water quality parameters and electrofisher settings. Both the U.S. Fish and Wildlife Service and the Canadian Department of Fisheries and Oceans offer courses on electrofishing that include consideration of adverse effects and ways to minimize them (e.g., Kolz et al., 1998). Many provincial or state (e.g., Colorado) and federal fishery workers are required or encouraged to take these courses. Some states have or are developing their own training programs and manuals (e.g., Wyoming; Meyer and Miller, 1995).

In California, where coho salmon and steelhead (sea-run rainbow trout) were listed throughout the state in 1996 as threatened or endangered Evolutionarily Significant Units under the federal Endangered Species Act, there is serious concern about the legal and ethical use of electrofishing for population surveys, monitoring, and scientific investigations (Nielsen, 1998). Nielsen (1998) reported that in response to these concerns, a workshop was convened in Ukiah, California, on 10 February 1998 by 48 federal, state, academic, tribal, industrial (timber), and fisheries-consultant organizations to discuss electrofishing guidelines and protocols. A draft of general recommendations from that meeting was still under review late in 1998, but Nielsen (1998) expressed concern that the recommendations would be inadequate to effectively limit use of electrofishing under any set of circumstances. Noting that the effective size of some salmon and trout populations or evolutionarily significant units can be very small (frequently less than 25 breeding pairs), she advocated requiring use of other, non-invasive, study methods when the cumulative effects of electrofishing over time might significantly reduce a population's ability to persist or result in loss of unique components in the genetic diversity of the species. Nielsen (1998) concluded by suggesting that "the American Fisheries Society should develop a set of guidelines for least-invasive sampling methodologies and adopt a policy on the ethical use of electrofishing. . . ." These guidelines and criteria could then be used by federal and state agencies to strictly (and uniformly) regulate potentially harmful electrofishing activities under their jurisdiction.

Manufacturers of electrofishing gear are obviously concerned about adverse impacts as well. They have a vested interest in the technique and have begun developing and marketing equipment intended to reduce electrofishing injuries. As examples, see the advertisements on both sides of the back cover of Fisheries 16(6), November–December 1991. One is for Coffelt Manufacturing's CPS (Complex Pulse System, a patented pulse train of three square pulses at 240 Hz repeated 15 times per second), which was specifically developed to reduce spinal injuries. The other advertisement is for Smith-Root, Inc.'s P.O.W. (Programmable Output Waveforms) unit, that allows users to select from a very wide range of patterns or waveforms, including pulse trains, some of which are likely to be less harmful than others (Meyer and Miller, 1995). More

Fig. 4. Bent backs and abnormal growth in west slope cutthroat trout (*Oncorhynchus clarki lewisi*) probably caused by electrofishing (top and middle photographs) with normal trout for comparison (bottom photograph). (All about 38–40 cm TL. Top two fish were the only obviously deformed specimens among 93 trout maintained as broodstock in Kiakho Lake, British Columbia, in June 1991. All fish were originally captured as 1 to 3-year-old juveniles a few years earlier by stream electrofishing, and that event was considered the most likely cause for the deformities. However, such deformities are sometimes attributed to other causes. Photographs provided by and reproduced with permission of G. Oliver, Kootenay Region, British Columbia.)

recently, Smith-Root, Inc. (1998) offered a special "sweeping" PDC waveform that progressively decreases duty cycle from 60 to 10% during the first 10 s each time the control unit is switched on by reducing either pulse width or frequency. The manufacturer suggested that this new waveform will minimize injury by reducing the percentage of time that electricity is applied as fish are attracted from cover to the anode.

Even theories regarding the causes and mechanisms of fish responses in electric fields are being reexamined in an attempt to identify and explain specific factors associated with injuries. During the workshop on electrofishing injury held in July 1991 as part of the annual meeting of the Western Division of the American Fisheries Society in Bozeman, Montana, N.G. Sharber introduced what has since often been referred to as the "Bozeman paradigm." His theory is that the observed responses of fishes in electric fields, including muscular seizures resulting in spinal and related injuries, represent essentially the same phases of epilepsy observed in

humans and other animals subjected to electroconvulsive therapy (Sharber et al., 1994, 1995; Sharber and Black, 1999). As discussed later under "Responses of Fish to Electric Fields," he correlates these epileptic phases–automatism, petit mal, and grand mal–with the more familiar and well-published descriptions and explanations of electrofishing responses, particularly those he refers to as the "Biarritz paradigm" espoused by Blancheteau et al. (1961); Lamarque (1963, 1967a, 1990); Vibert (1963, 1967b); and Blancheteau (1967) following their intensive investigations at the Biarritz Hydrobiological Station in France.

Another new theory views electrofishing as a power-related phenomenon (Kolz and Reynolds, 1989a; Kolz et al., 1998). Designated as A Power Transfer Theory for Electrofishing by Kolz (1989a), it explores the relationship between electrical power in water and in fish as a function of the ratio of conductivity of water to the effective conductivity of fish. This theory, like the Bozeman paradigm, is discussed later in more detail under "Responses of Fish to Electric Fields."

Interactions of fish, water, and electricity are a very dynamic, complex, and poorly understood mix of physics, physiology, and behavior. Perhaps because there are so many variables, Reynold's (1995) quote of W.G. Hartley seems particularly apropos for the field of electrofishing: "There are no experts, only those who have not been found out." This suggestion is not intended to discredit or belittle the extremely valuable contributions and knowledge of many researchers who have spent much of their lives studying the effects of electric fields on fish or using and developing electrofishing techniques but rather to indicate that, despite their efforts, we still have much to learn and many discrepancies to resolve. Noting that most recent research focuses on descriptive comparisons of electrofishing techniques and their injurious effects, Paul and Miskimmin (1997) recommended that future research include more carefully designed experiments to test clearly defined hypotheses. Reynolds (1995) suggested that researchers network worldwide "to unite the techniques of electric fishing and its theoretical foundation." Although that theoretical foundation is still far from complete, there is need for a coordinated program of future electrofishing research. Such a program should optimize resources at all levels, ensure comparability of data, and test validity of results through independent replication of experiments.

Results — Electric Fields in Water

Electrofishing (sometimes referred to as electric or electrical fishing, electroshocking, or simply shocking), as well as the use of electrical barriers, screens, and some forms of anesthesia, depends on the generation of a sufficiently strong electric field around or between electrodes in water to elicit the desired responses by targeted fishes. The size, shape, and nature of that field, as defined by the distribution of and changes in its electrical intensity, are determined largely by container or basin configuration and dimensions; conductivity of the water and bounding or surrounded media and substrates; position, size, and shape of the electrodes; and the peak electrical potential (voltage differential), type of current, and waveform generated between those electrodes. These factors were discussed extensively by Cuinat (1967); Novotny and Priegel (1971, 1974); Sternin et al. (1972, 1976); Halsband and Halsband (1975, 1984); Smith (1989); Novotny (1990); Meyer and Miller (1995); Reynolds (1996); and Kolz et al. (1998).

Water Conductivity

Water conductivity, water's capacity to conduct an electric current, is the most critical environmental factor in establishing an electrofishing field. The conduction of electricity (electrical energy) in water is an ionic phenomenon. Conveyance of negative charges via electrons from negative to positive electrodes (cathode to anode) to complete an electrical circuit depends on electrolytic reactions at the electrodes and an almost instantaneous chain of ionic movements and interactions (exchange of electrons) in the water between and around the electrodes. Accordingly, conductivity varies directly with the nature and concentration of ions (charged atoms and molecules, mostly from dissolved solids and dissociated water). In nearly pure water, which has a very low conductivity, ionization of water itself furnishes a substantial portion of the conducting ions. When electrofishing in very low-conductivity streams with inadequate power supplies, salt is usually added to water upstream of the sampling area to artificially increase its conductivity (Lennon and Parker, 1958; Zalewski and Cowx, 1990).

Conductivity is the reciprocal of resistivity (ohms-cm), a term preferred by some authors, especially for very low-conductivity (high-resistivity) waters. Conductivity is usually measured with a conductivity meter as mhos or siemens (S) per cm (usually µmhos/cm or µS/cm; μ = micro or 10^{-6}). (Mho is ohm spelled backward to indicate the inverse relation between these units.) Following the International System of Units, the unit name siemens is used in the remainder of this report.

Conductivity in natural waters ranges from as low as 5 µS/cm in pure mountain streams (Gatz et al., 1986; Zalewski and Cowx, 1990) to 53,000 µS/cm in sea water (Omega Engineering Inc., 1990). The upper limit for potable

water is about 1,500 µS/cm (Wydoski, 1980). Conductivity in a particular body of water, although generally quite uniform, can vary considerably from one location to another depending on substrate composition and especially the inflow of tributaries or effluents of highly different conductivities.

Ambient water conductivity also varies with water temperature. As temperature rises, water viscosity decreases and ionic mobility and solubility of most salts increase. Rates of change in conductivity depend on ionic content and vary from about 5.2% per degree C for ultrapure waters to 1.5% per degree C for acids, alkalis, and concentrated salt solutions (Omega Engineering Inc., 1990). For natural waters between 10 and 25° C, the coefficient is approximately 2 to 2.3% per degree C. To approximate water conductivities at various temperatures within this range, Reynolds et al. (1988), Reynolds (1996), and Kolz et al. (1998) used the equation $c_2 = c_1 / (1.02^{(t1-t2)})$, and Sternin et al. (1972, 1976) used $c_2 = c_1 / (1 + 0.023(t_1 - t_2))$, where c is conductivity and t is temperature. It is important to record whether measured or reported water conductivity is ambient (actual value for the temperature at which it was measured) or specific (value normalized to 25° C); if the latter, it needs to be recalculated for ambient (actual) temperature.

Electrofishing Currents and Waveforms

There are two principal types of electrical currents, but interrupted or pulsed variations of one are sufficiently different and important to be treated effectively as a third type. Bipolar or alternating current (AC) is characterized by continually reversing polarity and movement of electrons or ions of like charge (Fig. 5A). Unipolar or direct current (DC) is characterized by movement of electrons or ions of like charge in one direction (Figs. 5B–J). However, as used hereafter, DC specifically refers to a continuous unipolar current of constant voltage (smooth or straight DC, Fig. 5B) or nearly constant voltage (rippled DC, Fig. 5C). When a unipolar current is periodically interrupted or pulsed, it is specifically referred to as the third type of current, pulsed DC (PDC; Figs. 5D–I). AC also can be pulsed, but pulsed AC (e.g., Jesien and Hocutt, 1990) is rarely used for electrofishing.

For AC and PDC, changes in voltage amplitude or differential (current intensity) over time define the shape (graphical form as displayed by an oscilloscope) and frequency (Hz—hertz = cycles, pulses, or pulse patterns per second) of their waveforms. Although other AC waveform shapes and frequencies are possible, AC used for electrofishing usually consists of a sinusoidal waveform at a fixed frequency of 50 or 60 Hz (single-phase generator), 180 Hz (three-phase generator), or higher (e.g., 300 or 400 Hz) as a function of generator speed (Novotny and Priegel, 1974; Novotny, 1990).

Depending on how they are produced, PDC waveforms used for electrofishing occur in a variety of shapes, most commonly square (rectangular), half-sine, quarter-sine, or exponential, and can be delivered over a wide range of frequencies, usually between 15 and 120 Hz, but at least experimentally from 1 to about 500 Hz. Pulse-frequency pattern can be either simple (uniform) or complex, the latter usually consisting of a high primary frequency interrupted secondarily at a much slower frequency to produce bursts, packets, or trains of the higher-frequency pulses (Fig. 5I).

PDC waveforms also are characterized by pulse width (time current flows during each pulse, usually expressed in ms, milliseconds) and duty cycle (percentage of time current actually flows from the beginning of one simple pulse or complex pulse-pattern to the next). For simple PDC, duty cycle is a function of pulse frequency and width. As frequency in a PDC is increased, a constant pulse width results in a greater duty cycle, whereas a constant duty cycle results in a proportionately shorter pulse width.

In modern electrofishing, DC is usually produced by conditioning power from an AC generator, or a battery and inverter, with transformers, rectifiers, and filters (Novotny, 1990; Novotny and Priegel, 1971, 1974). DC produced by true DC generators is smooth (Fig. 5B), whereas that produced by filtering rectified current from an AC generator tends to be at least slightly rippled (Fig. 5C). However, DC generators are heavier, more expensive, less flexible in voltage control, and less reliable than AC generators with comparable power ratings. DC produced by a three-phase AC generator is already relatively smooth and requires much less conditioning than that produced by a single-phase AC generator.

In most cases, PDC waveforms also are produced from rectified AC. Rectified sinusoidal AC directly produces half-sine PDCs at either the same or twice the AC frequency, depending on whether the current is half or full-wave rectified (Figs. 5D and E). Mechanical or electronic choppers (pulsators) are used to generate quarter-sine and exponential or capacitor-discharge waveforms (Figs. 5G and H) from unfiltered rectified AC or square waveforms (Fig. 5F) from rectified AC that has been first filtered to produce DC. Square waveforms are perhaps the easiest to adjust in pulse width and frequency. Some very flexible electrofishing control units provide AC, DC, and PDC–the latter with variable pulse frequencies, widths, and sometimes shape. Some systems allow or incorporate secondary switching or interruption of PDC to produce complex pulse frequencies (e.g., University of Wisconsin Engineering and Technology Center's Quadrapulse, Smith-Root's P.O.W., and Coffelt's CPS).

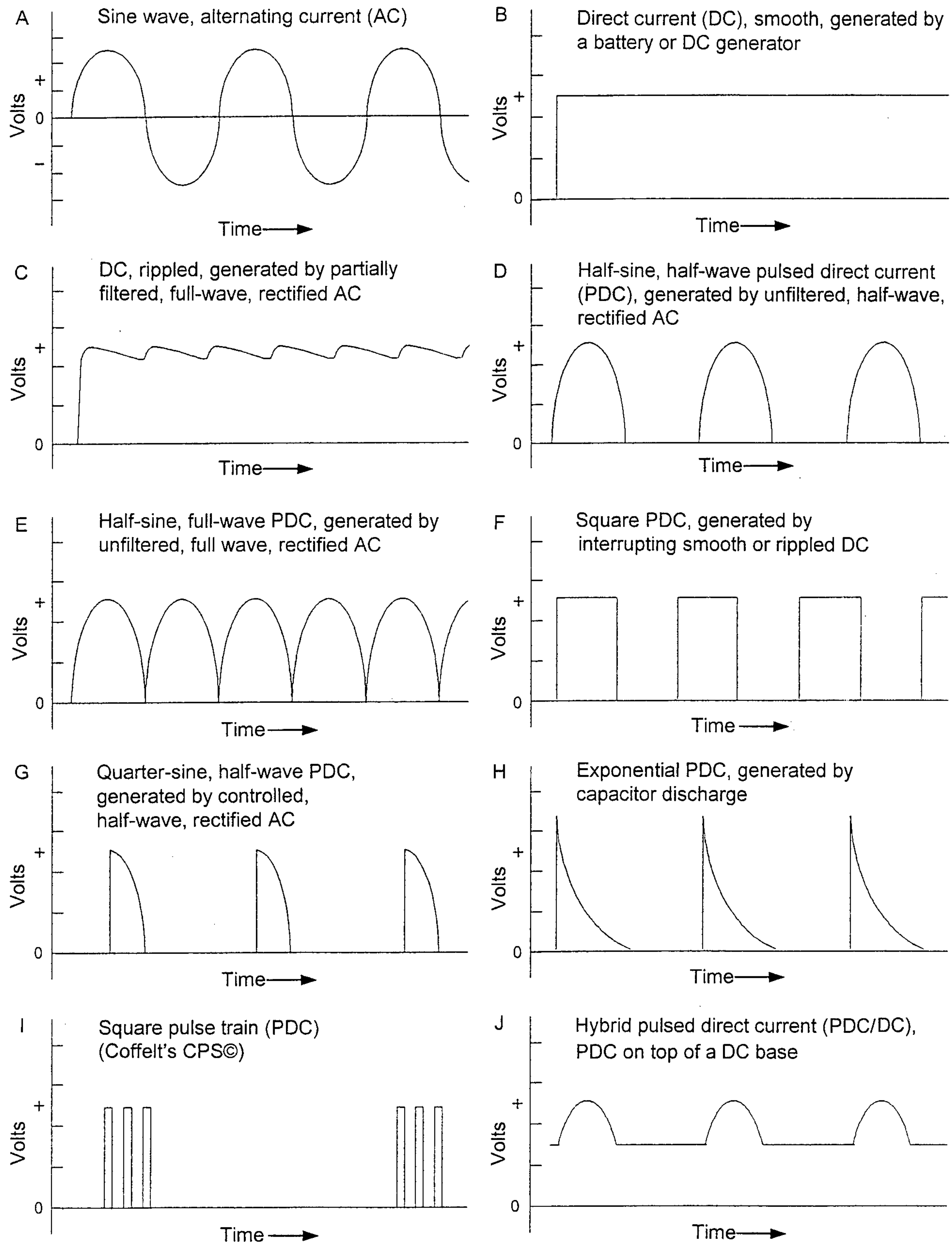

Fig. 5. Selected waveforms used in electrofishing.

Such pulse-train waveforms were suggested by Haskell et al. (1954) over 45 years ago. PDCs are often favored for electrofishing because they require much less-powerful generators or batteries than DC, and often AC, to create electric fields of comparable size and effectiveness.

Through various manipulations of the current, DC and PDC have even been hybridized to produce a PDC on top of DC (Vincent, 1971; Fredenberg, 1992; Fig. 5J). In such currents, the pulses drop only to a preset minimum voltage level when switched off rather than to zero volts. Strongly rippled DC (weakly filtered, rectified AC) could be considered a hybrid current.

The various PDC waveforms generated by electrofishing control boxes are sometimes characterized by anomalies in the expected shape. For example, Fredenberg (1992) reported spikes at the leading or trailing ends of square-waveform pulses; Van Zee et al. (1996) documented under test conditions the presence of a trailing voltage spike 50 to 60% higher than the rest of a square-waveform pulse followed immediately by a small exponential pulse of reverse polarity (magnitude 20% of unspiked pulse voltage); and Sharber and Carothers (1988) described small, rounded, secondary pulses immediately following pulses in a 60-Hz, exponential waveform. In the latter example, Sharber and Carothers (1988) suggested that the small secondary pulse was of sufficient voltage near the anode to produce essentially a 120-Hz, mixed waveform that enhanced the immobilization of fish.

Jesien and Hocutt (1990) noted that nominally square PDC waveforms (Fig. 5F) generated by their equipment changed shape as water conductivity increased. At conductivities of about 100 µS/cm, the trailing edge was not perpendicular, and the voltage level was not constant across the top of the pulse. An exponential-like voltage spike became evident at 1,000 µS/cm and was especially prominent at 10,000 µS/cm. In contrast, they found that characteristics of their pulsed AC waveforms remained constant with changes in water conductivity. Kolz (personal communication) suggested that they may have used a faulty power source for their square-wave PDC.

Because output waveforms are not always as expected based on control box settings, it is important to periodically calibrate, verify, and document waveform in the output circuit with an oscilloscope. For example, an oscilloscope tracing illustrated by Van Zee et al. (1996) for square-wave PDC generated with control-box settings for 80 Hz and 50% duty cycle revealed an actual frequency of 73 Hz and duty cycle of 64%, as well as the trailing spike and negative secondary pulse described above.

Review of the published literature and personal communications revealed that authors and biologists frequently fail to note the type of current and waveform used in electrofishing. Even when noted, some descriptions of the current are incomplete, misleading, or erroneous. PDC is often simply referred to as DC, reflecting its unipolar but not its pulsed nature. Also, referring to its typical origin via an AC generator, PDCs are sometimes incompletely called "rectified AC," which more specifically refers to either of the two half-sine PDC waveforms (Figs. 5D and E) or, when filtered or originating from 3-phase AC, rippled DC (Fig. 5C). Even the term "pulsed AC" has been improperly used for PDC. For example, Hill and Willis (1994) used a current which they and an early manual for the Coffelt VVP-15 electrofishing control unit referred to as pulsed AC. Hill and Willis (1994) described it as the positive half of a sinusoidal AC waveform, and the manual illustrated it as quarter-sine PDC (Fig. 5G) but mislabeled it as pulsed AC (Van Zee et al., 1996; the error has been corrected in more-recent versions of the Coffelt manual). Furthermore, an oscilloscope tracing of this waveform by Van Zee et al. (1996) closely approximated a square-wave PDC, possibly a slightly compressed quarter-sine waveform with the trailing margin squared off near the top.

Field Intensity

The responses of fish to electric fields in water are dependent, at least in part, on the field's strength or intensity. Field intensity can be described by any of three interrelated quantities: voltage gradient, current density, or power density. The relations between these descriptors of field intensity and water conductivity are illustrated in Figs. 6, 7, and 8.

Voltage gradient (E) is the average voltage differential per unit distance along lines of current or flux between two isopotential surfaces and is usually expressed as volts per centimeter, V/cm. Voltage is the amount of potential energy stored per unit of electrical charge, expressed as volts (V, joules/coulomb). Lines of flux (or current) represent the net directions or paths of current in an electric field around and between electrodes of opposite polarity. An isopotential surface lies perpendicular to the lines of flux and is defined by a set of points having the same voltage differential from the surface of the electrode. If the water is of uniform conductivity and unbounded for a sufficient distance in all directions (an unlikely condition), the electrode is spherical, and other electrodes are sufficiently distant, at least the isopotential surfaces near the electrode can be visualized as shells, all points of which are the same distance from the surface of the electrode.

Voltage gradient can be physically measured in the water or approximated by calculation based on output voltage, the surface area, size, and shape of the electrodes, the distance between them, and proximity of bounding or surrounded surfaces or media of different conductivity. For practical purposes, the distribution of

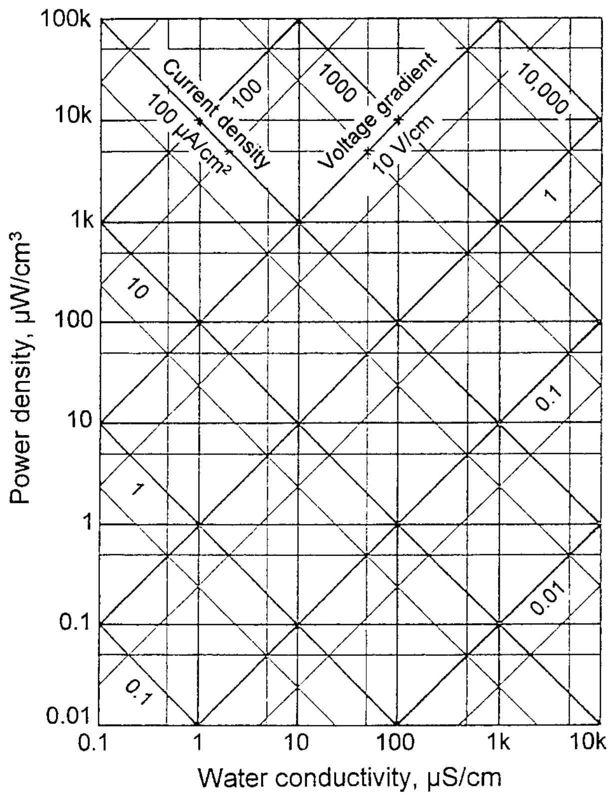

Fig. 6. Four-way logarithmic graph of relations among measures of electrical-field intensity (power density, current density, and voltage gradient) relative to water conductivity. Reproduced with permission from Fig. 7 in Kolz, 1989a; axis labels modified.)

voltage gradient near and between electrodes is independent of (unaffected by) water conductivity if that water conductivity remains uniform (unstratified) in proximity to and between the electrodes and other parameters (e.g., basin, electrodes, voltage differential between electrodes) are identical. Under such conditions, a map of voltage gradient would be the same whether water conductivity was 10 or 1,500 µS/cm. However, this would not be true if water conductivity was stratified as in an estuary or at and just downstream of a tributary, spring, or industrial outflow of substantially different conductivity.

Current density (J) is usually expressed as microamperes or milliamperes per square centimeter, µA/cm^2 or mA/cm^2, respectively ($\mu = 10^{-6}$, $m = 10^{-3}$), and described as the amount of current passing through a unit area of isopotential surface (perpendicular to the lines of flux). Current is the quantity of electrical charge flowing per unit time, usually expressed as amperes (A, coulombs/sec). Since instruments have not yet been developed for direct measurement of current density, it must be calculated ($J = cE$).

Power density (D) is the amount of power dissipated per unit volume between two isopotential surfaces. Power, the mathematical product of voltage and current, is the amount of energy expended per unit time, usually expressed as watts (W, joules/sec). Similarly, power density is the mathematical product of voltage gradient and current density, and it is usually expressed as microwatts per cubic centimeter, µW/cm^3. Because it is a function of current density, power density is also dependent on water conductivity. Like current density, instruments have not yet been developed for direct measurement of power density, and it too must be calculated ($D = JE = cE^2 = J^2 / c$). Although reintroduced to electrofishing literature a decade ago by Kolz (1989a), the term "power density" was perhaps first introduced and used in North American literature by Monan and Engstrom (1963). Power density, or the volumetric expression of power it represents, was also used or discussed by Adams et al. (1972) and Sternin et al. (1972, 1976).

Kolz (1989a) and Kolz and Reynolds (1989b, 1990a) used a unique 4-way logarithmic graph of water conductivity, voltage gradient, current density, and power density (Fig. 6) to help explain their theory of power-density transfer (discussed below) and for overlaying graphs of in-water field-intensity thresholds for observed responses of fish to electric fields. Any point on the graph simultaneously represents the corresponding values for each quantity, and knowing any two quantities (e.g., conductivity and voltage gradient) provides a quick alternative to calculation for approximating the remaining two quantities. Many interesting relations between these factors are revealed by studying the graph. For example, when voltage gradient is held constant, both current density and power density increase in direct proportion to water conductivity. At any point on the graph for which voltage gradient is 1 V/cm, the numeric values for both current density and power density are equal to water conductivity.

The relation between voltage gradient and current density relative to water conductivity at a constant power density of 100 µW/cm^3 can be visually explored in Fig. 7. The upper and middle graphs are essentially the same except that the upper graph uses logarithmic scales for both axes, and the middle graph uses an arithmetic scale for the Y-axis. The range of conductivities of particular concern in fresh waters, about 10 to 1,500 µS/cm, is bounded by dotted vertical lines in both of these graphs and represented exclusively in the bottom graph for which all axes are arithmetic with separate Y-axis scales for current density and voltage gradient. Because of the inverse relation between current density and voltage gradient relative to conductivity ($c = J / E$), the curve for

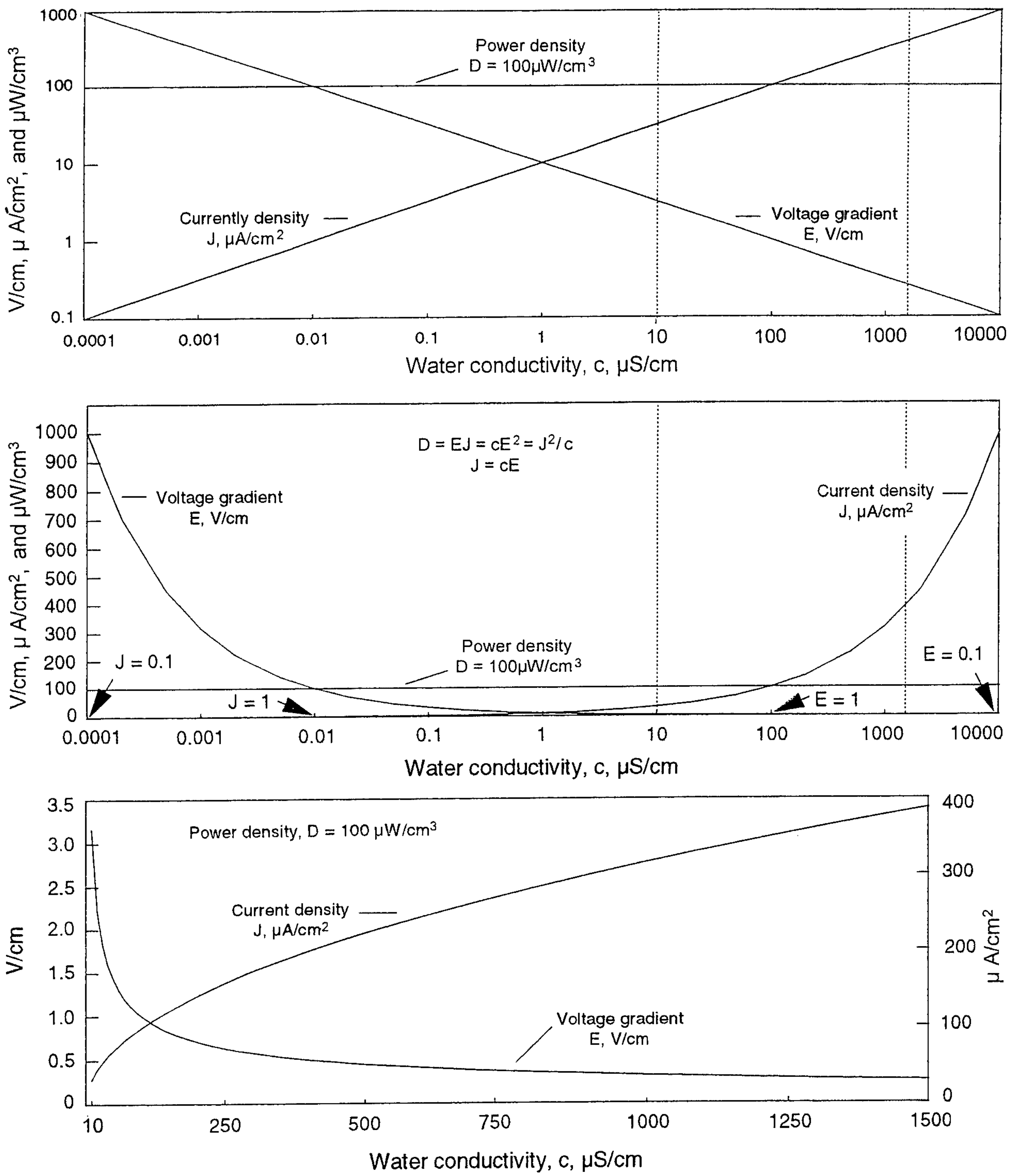

Fig. 7. Changes in voltage gradient and current density relative to water conductivity at a constant power density of 100 μW/cm^3. (Top and middle graphs are the same except the Y-axis is logarithmic in the top graph and arithmetic in the middle graph. Bottom graph is limited to the range of conductivities typical of fresh waters and bounded by dotted vertical lines in the upper graphs; both axes are arithmetic with different Y-axis scales for voltage gradient and current density.)

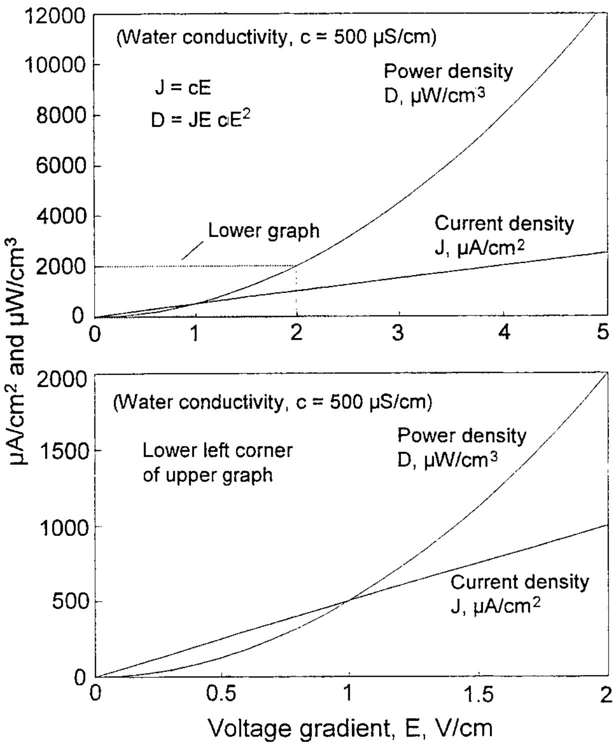

Fig. 8. Changes in current density and power density relative to voltage gradient in water with a conductivity of 500 μS/cm. (For other conductivities, adjust the values along the vertical axis in direct proportion to the change in conductivity—e.g., for half the conductivity, 250 μS/cm, halve the values along the Y-axis.)

voltage gradient in the middle graph of Fig. 7 becomes asymptotic with the Y-axis as conductivity approaches zero and asymptotic with the X-axis as conductivity approaches infinity, whereas the situation is reversed for current density. As a result, the curve for voltage gradient at a fixed power density is relatively flat over all but the lower end of the range for conductivity in fresh waters (bottom graph of Fig. 7) and practically horizontal for more saline waters. The relative stability of voltage gradient in medium- to high-conductivity fresh waters has important implications with respect to field-intensity response thresholds and standardization of electrofishing fields (discussed later in this review).

Changes in current density and power density relative to voltage gradient at a constant water conductivity of 500 μS/cm are illustrated in Fig. 8 (the lower graph is an expansion of the lower left corner of the upper graph). Note that the values for current density, power density, and water conductivity are equal when voltage gradient is 1 V/cm (as in Fig. 6), and, as predicted by their definitions, current density increases linearly and power density geometrically with voltage gradient. For values of voltage gradient less than 1 V/cm, power density is less than current density.

For PDC and AC, in-water measures or calculations of peak field intensity (maximum voltage gradient, current density, or power density through one or more waveform cycles) are substantially greater and probably more biologically significant (Kolz and Reynolds, 1989b) than corresponding values of mean PDC or rms AC field intensity. For sinusoidal AC (Fig. 5A), peak voltage gradient and output voltage are approximately 41% greater than corresponding rms values ($V_p = 1.41 \times V_{rms}$). Root-mean-square values are necessary for AC because mean voltage would be zero. Concern that positive peak to negative peak voltage differential in AC might be even more biologically significant than peak voltage differential from zero or base level is unwarranted; the negative portion of the waveform represents a reversal in current direction rather than negative voltage per se (however, fish are polarity sensitive and accordingly some responses differ when subjected to alternating or unidirectional currents of comparable peak voltage). For square PDC waveforms (Figs. 5F and I), mean voltage varies directly with duty cycle (percentage of on time); for example, with a 25% duty cycle, peak voltage is four times greater than mean voltage. For other PDC waveforms (Figs. 5D, E, G, and H), mean voltage varies according to their shape as well as duty cycle. For smooth DC, peak and mean values for field intensity or electrical output are identical.

To facilitate comparisons, researchers and authors must specify whether measures of field intensity or output (voltage, amperage, power) for PDC or AC are peak or mean (rms in AC) values. Meters on most electrofishing control boxes register mean output values for PDC or rms output values for AC (e.g., volt and ammeter on Coffelt's VVP-15 and ammeter on Smith-Root's GPP 5.0), whereas meters on very few units register peak output (e.g., ammeter on Coffelt's Mark XXII which generates CPS). Also, biologists should not rely on the accuracy of control box settings and meters without periodic calibration. Van Zee et al. (1996) revealed that voltmeters and ammeters included on some electrofishing control units (e.g., Coffelt's VVP-15) are meant to serve as references for relative or consistent settings rather than provide accurate measures of output. For example, using a boat-electrofishing system with a control box adjusted for an output of 230 V and 2 A for each of two currents, they reported oscilloscope measures of peak output to be 280 V and 1.7 A for a quarter-sine-wave PDC and 250 V and 1.5 A for square-wave PDC. The latter current also was set for 80 Hz with a 50% duty cycle, but the oscilloscope

documented a pulse frequency of 73 Hz and a 64% duty cycle. In addition to field intensity and output, biologists should document water conductivity and temperature and adequately describe or verify the waveform (shape, frequency, pulse width, duty cycle), electrodes (position, size, and shape), and operating procedure.

Voltage gradients are best measured in water with an appropriate voltmeter or oscilloscope connected to insulated wires, the tips of which are exposed and set a fixed distance apart (Kolz, 1993; Kolz and Reynolds, 1990b; Kolz et al., 1998). The maximum voltage differential per unit distance measured with this probe at any particular location is the voltage gradient and will be obtained when the exposed tips are oriented along the field's lines of flux (the principal direction of current flow in three dimensions around and between electrodes). When the probe tips are rotated horizontally and vertically precisely perpendicular to the lines of flux (along an isopotential surface), there will be no voltage differential, and the voltmeter or oscilloscope will register zero volts. Voltage gradients can also be approximated as the difference between voltages measured from the electrode to two sufficiently close points in the water (Kolz, 1993; Kolz and Reynolds, 1990b; Kolz et al., 1998). Like voltage-gradient probes, fish are subject to the greatest voltage differential when they are oriented along the lines of flux. This is often referred to as "head-to-tail voltage." Fish are subject to the least voltage differential when oriented perpendicular to flux lines.

Voltmeters specifically designed to measure peak voltage (e.g., peak-voltage detectors; Jesien and Hocutt, 1990) or oscilloscopes should be used for accurate measurements of peak voltage gradient at specific reference points in PDC (or pulsed AC) fields. However, the presence of voltage spikes in a PDC waveform (discussed earlier) can affect readings in some peak-voltage detectors. Oscilloscopes, although more expensive, allow the user to observe voltage spikes and differentiate such from normal peak voltages or voltage gradients by ignoring any spikes, as well as to monitor other waveform characteristics (e.g., shape, pulse frequency, pulse width, and duty cycle). A typical voltmeter (or multimeter) can be used to measure the constant voltages or voltage gradients at specific reference points in smooth DC fields (peak = mean) and rms voltages or voltage gradients in AC fields. But according to Jesien and Hocutt (1990) and Fredenberg (personal communication), such meters cannot accurately measure either peak or mean voltages in PDC or pulsed AC. For the latter, either an oscilloscope or special instrumentation (e.g., peak-voltage detector) is required (Kolz, 1993). However, if a smooth DC or AC field can be temporarily substituted using the same system and peak output, the DC voltage or voltage gradients measured or peak values calculated from AC rms measurements made with a standard voltmeter in that field should be identical to peak voltages or voltage gradients in the corresponding PDC or pulsed AC field.

Heterogeneous and Homogeneous Fields

Because the basins occupied by rivers, streams, lakes, reservoirs, and most other waters are irregular in shape, and their cross-sectional areas are much larger than the electrodes, electrofishing fields generated therein are heterogeneous. In such fields, lines of flux (current) can be visualized as radiating from and spreading widely around and between the electrodes (Fig. 9). Field intensity is greatest next to the electrodes and decreases to barely perceptible levels as distance from the electrodes increases, even in the area directly between anode and cathode when they are sufficiently separated. The actual field intensity encountered by a fish in a heterogeneous field depends on the fish's location in the field.

Homogeneous fields are typically restricted to laboratory settings in raceways, troughs, or tanks with a constant cross-sectional profile and electrodes approximating that profile at each end of the desired field. In homogeneous fields, the current flows parallel to the sides of the container directly from one electrode to the other. Except adjacent to bounding surfaces or substrates, this arrangement provides a constant voltage gradient, current density, and power density regardless of location between the electrodes.

Controlled experiments in homogeneous fields allow relatively precise control of field intensity and eliminate many of the electric-field variables that are encountered in natural waters. This greatly simplifies experimental conditions and facilitates determination of cause and effect, but results may be difficult to extrapolate to normal electrofishing operations.

Bounding or Surrounded Media and Substrates

Depending on their porosity and conductivity, the bounding media or substrates of a body of water can affect the distribution of electricity in that body of water (Sharber et al., 1995). The conductivity of bottom substrates can vary considerably with location, even in the same water body. Haskell (1954) and Zalewski and Cowx (1990) reported that substrates of fine particles and organic debris are more conductive than those of coarse gravel and rubble. Because of substrate and interstitial water conductivity, electric fields can extend well into the bottom substrate and even onshore. Riddle (1984) suggested that a person standing barefoot on a bank

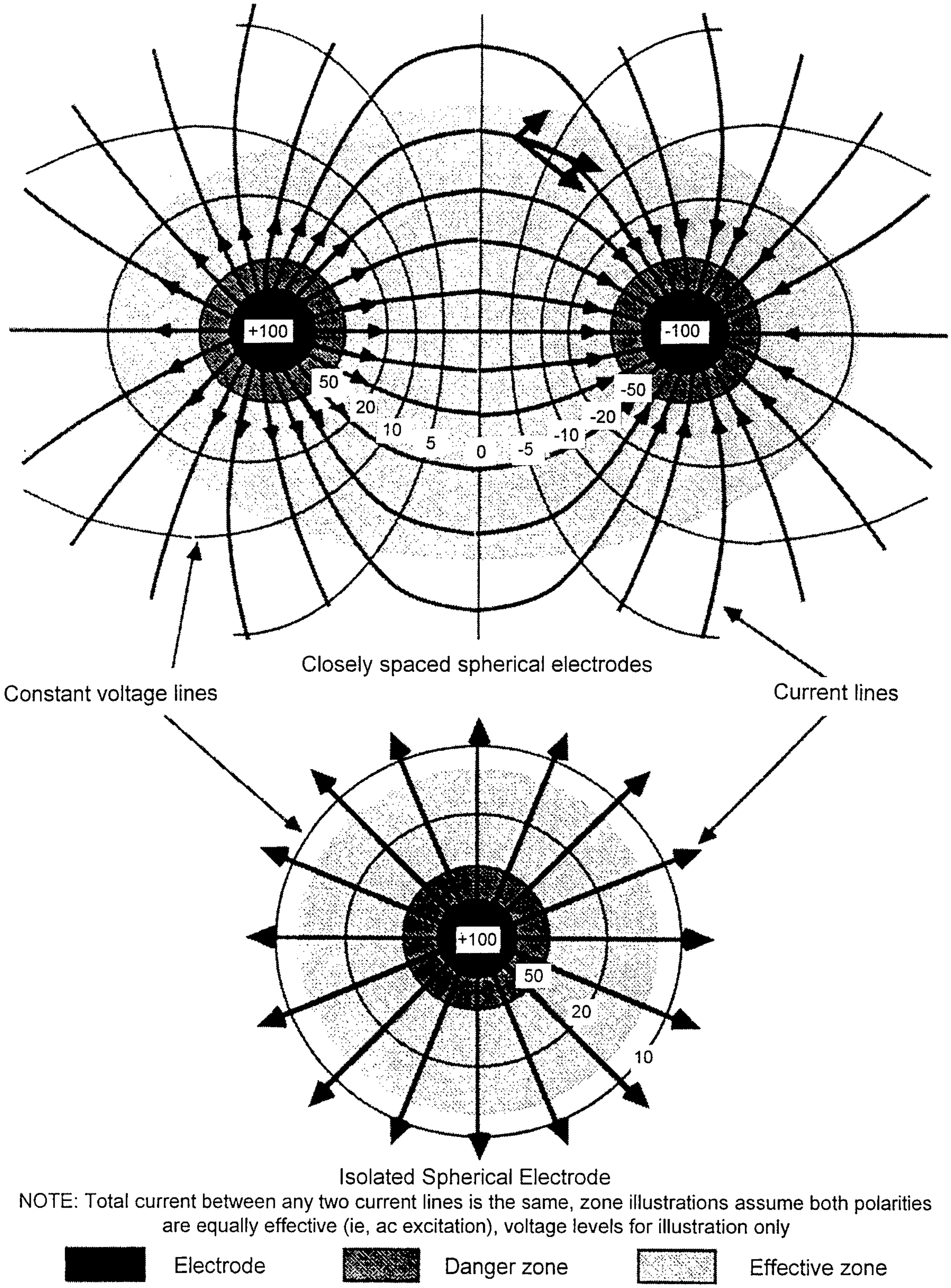

Fig. 9. Hypothetical two-dimensional diagrams of heterogeneous electric fields around and between electrodes. (When electrodes are sufficiently far apart, the field around each is essentially isolated as indicated in the lower diagram. Voltage is relative to that of the water where voltage gradient is minimal. Constant-voltage (isopotential) lines are perpendicular to the radiating lines of current. Contrary to the diagrams, current flows from negative to positive electrodes. Reproduced with permission from Fig. 3.10 in Novotny, 1990.)

could be shocked. Some of the first electrofishing systems in the United States were shore-based and used AC with one electrode or electrode array implanted in the ground along shore (Haskell, 1940, 1950, 1954); this practice is still used today, including DC and PDC systems with buried cathodes. Smith (1991) described an experimental electric shark barrier that also incorporated electrodes implanted onshore rather than directly in the water.

Interactions between water and a bounding or surrounded medium or substrate of different conductivity apparently cause water conductivity near the interface to progressively increase or decrease toward that of the adjacent surface with corresponding changes in current density and voltage gradient ($c = J / E$). If the adjacent medium or substrate is more conductive than the water some distance away, the current in the water near its surface progressively concentrates (current density increases) as voltage gradient correspondingly declines (perhaps hypothetically, such that power density ($D = JE$) remains the same at each point as it would have been in the absence of the adjacent medium or substrate). Conversely, current density is reduced and voltage gradient intensified immediately along or around less-conductive media, including air at the water surface (Zalewski and Cowx, 1990). As documented by Haskell (1954) and noted by many others since, fish themselves distort the field in their immediate vicinity if they are more or less conductive than the water (Fig. 10).

Except when used as the cathode, Riddle (1984) recommended that metal boats not be used for electrofishing. He suggested that if a conductive vessel is positioned between the electrodes, it would interfere with the field (concentrate the current and thereby alter field size and shape) and might adversely affect electrofishing efficiency. According to Sharber (personal communication), when a metal boat is situated in an electric field and not used as the cathode, it has an intermediate electric charge, negative with respect to the anode and positive with respect to cathode. This concern seems to have been overlooked in much of the literature on boat electrofishing, although some, especially earlier, workers strongly discouraged use of metal boats for reasons of safety (Goodchild, 1990, 1991).

Electrodes — Position, Size, Shape, and Other Matters

According to Novotny (1990), the electrodes are the most crucial part of an electrofishing system. Their spacing, size, surface area, and shape, along with water conductivity, determine the electrical resistance of the system and, for a specified voltage output, the distribution of field intensity that determines the unconfined size and shape of the effective field. Electrode systems that are inappropriate for the power supply and waters to be sampled can result in poor electrofishing efficiency or unnecessary harm to fish. Novotny and Priegel (1974) listed the following desirable characteristics for an effective electrode system:

- establishment of the largest region of effective electric current distribution in the water to be sampled,
- avoidance of local regions of unnecessarily large current densities, which waste power and are potentially harmful to fish,
- adjustable to meet changes in water conductivity,
- ability to negotiate weeds and obstructions,
- ease of assembly and disassembly, and
- avoidance of unnecessary disturbance to water to permit clear visual observation of fish.

When electrodes are positioned sufficiently far apart (more than several radii in the case of spherical electrodes–Novotny, 1990; 10 to 20 radii for rings–Smith, 1989), the field around each electrode is effectively independent and has no significant interactive effect on electrode or system resistance. The water outside well-separated anodic and cathodic fields is considered to be at "ambient potential" because its electrical potential does not vary significantly (its voltage gradient is nil–Cuinat, 1967). Fish that remain in water of ambient potential, even between the electrodes, are theoretically unaffected by the electrofishing operation. The level of ambient potential relative to the electrodes depends on voltage output, total resistance (sum of anodic and cathodic resistances), and the ratio of anodic to cathodic resistances (Kolz, 1993).

Novotny (1990) emphasized that "the most common electrode problem is that the electrodes are simply too small . . . .". At the same output voltage, larger electrodes have less electrical resistance in water and radiate larger electric fields but with lower maximum field intensity immediately around them. Larger electrodes thereby reduce the zone of tetany and extend the effective field for taxis (DC and PDC fields) and narcosis (see definitions and discussion later under "Major Intensity-Dependent Responses"). Increasing the number of anodes or cathodes in a system has a cumulative effect similar to increasing the size of an individual electrode. Maximum size or number of anodes or cathodes is dictated largely by practical considerations (e.g., maneuverability, transportability, interference with netting) and, especially in high conductivity waters, by generator capacity. When water conductivity is high, the size of the electrodes must sometimes be reduced to prevent generator overload.

To minimize cathodic effects on fish when using DC or PDC, cathodes should be as large as practical relative to anodes. This will also desirably maximize anodic field intensity and reduce the overall electrical resistance of

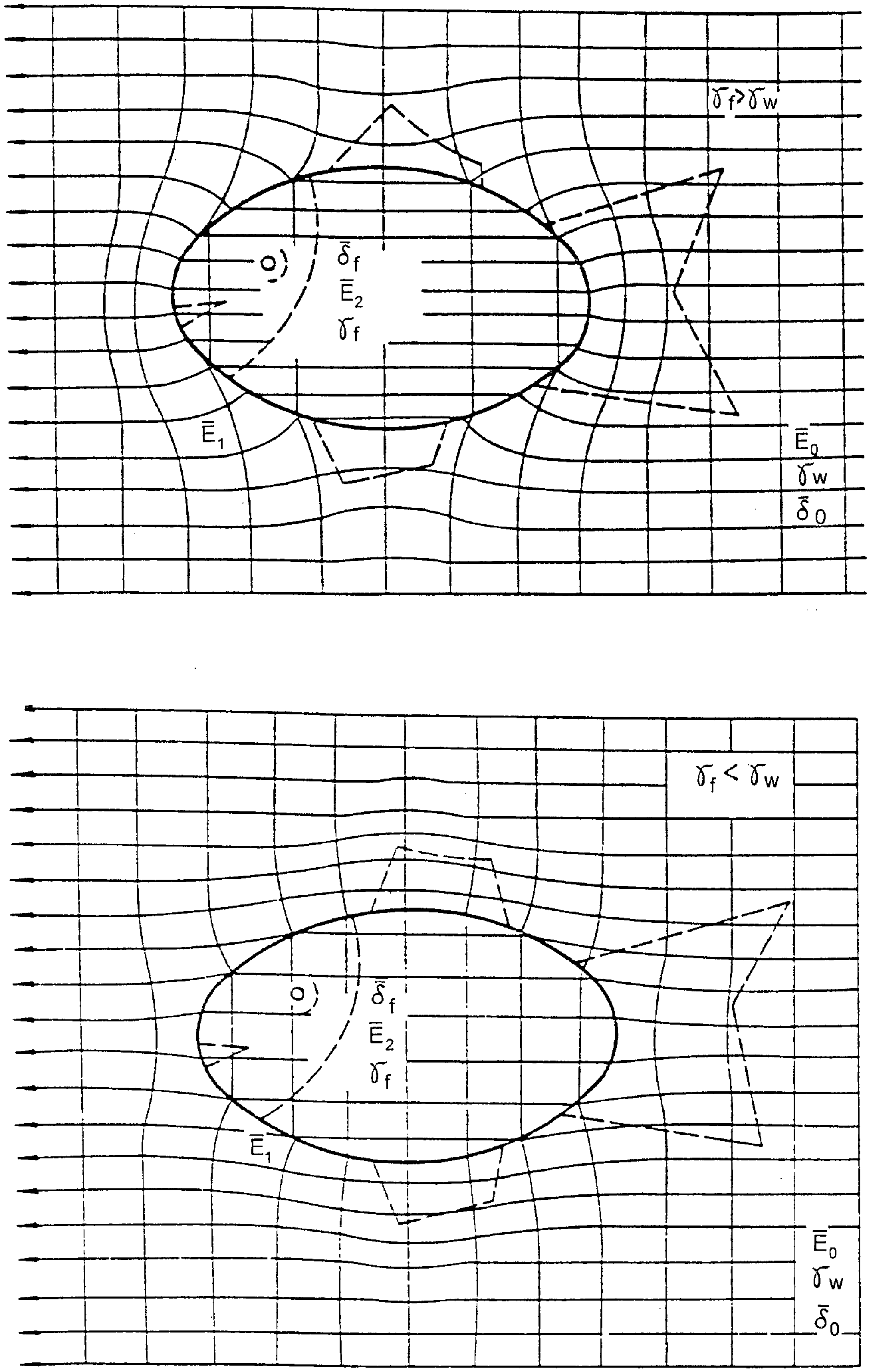

Fig. 10. Distortion of homogenous electric fields around fish in water that is less conductive (top) and more conductive (bottom) than the fish. (Horizontal lines are current (flux) lines and vertical lines are constant-voltage (isopotential) lines. Symbol γ = conductivity (c), E = voltage gradient, and δ = current density (J). Reproduced from Figs. 77 and 78 in Sternin et al., 1976.)

the system. When cathodes are larger than anodes, most of the total potential between electrodes is associated with the anode, and the voltage differential between anode and ambient potential is proportionately greater than between ambient potential and cathode. If cathodes are very much larger than anodes, the very low voltage differential between the cathode and soil and water in the vicinity may reduce the risk of severe shock or electrocution to people or animals that inadvertently approach or touch the cathode (Smith, 1989). Because cathodic resistance for well-separated electrodes is halved each time the surface area of the cathode is doubled, Smith (1989) suggested that 10 m^2 may be a practical limit to the size of the cathode. However, according to Temple (personal communication), A. Kolz maintains that in shore-based systems with buried cathodes, the earth itself becomes a very large cathode. With appropriate equipment and wiring on metal boats, cathode size is often maximized for DC or PDC electrofishing systems by using the boats themselves as cathodes (Kolz, 1993; Reynolds, 1996); on fiberglass vessels, cathode size is sometimes maximized by mounting large metal plates on their bottoms (Vibert, 1967b).

Kolz (1993) discussed the importance of and procedures for determining electrode and system resistance as well as making in-water measurements for mapping field intensity around and between various types of electrodes. Such data are necessary for comparing electrodes of various shapes, sizes, and designs, optimizing electrofishing efficiency, minimizing hazardous field intensities, and standardizing electrofishing fields. Kolz (1993) emphasized that electrofishing fields generated through different electrode systems cannot be standardized only by output voltage, current, or power. The distribution of field intensity around and between electrodes depends in large part on the specific size, shape, and configuration of those electrodes and must also be known or measured.

To this end, Kolz (1993) determined and compared the electrical resistance and voltage-gradient and voltage-differential profiles for 18 commonly used electrodes, including spheres, cylinders, horizontal loops, Wisconsin-ring dropper arrays, and vertical plates of various sizes. Measurements were taken in a concrete canal (water 1.4 m deep, 3 m wide) with matching electrodes 4 m apart (except for cylindrical electrodes which were 2.7 m apart), water conductivities of 111 to 190 µS/cm, and an electrical output of 100 V_{rms}. Electrical resistance data were normalized for a water conductivity of 100 µS/cm but can be adjusted by calculation for different water conductivities (electrode resistance is inversely proportional). Similarly, voltage-gradient and voltage-differential profile data for each electrode can be calculated for different applied voltages (directly proportional; for unmatched electrodes data must also be adjusted by the inverse ratio of their electrical resistances).

Spherical electrodes are considered electrically superior to other shapes (e.g., cables or narrow cylinders) and allow more accurate calculation of electrode resistance and voltage gradient maps. Electric fields generated immediately around well-submerged spheres are uniform and without the hot spots (localized regions of higher intensity) produced near the corners and edges of many other electrode shapes. For example, according to Sharber et al. (1995), charge is not distributed uniformly over long thin electrodes but concentrated at their distal ends. Except near their surfaces where tetanizing voltage gradients may exist, Novotny and Priegel (1974) and Novotny (1990) suggested that circular and ringlike electrodes, including dropper arrays, produce electric fields similar to those of spheres. However, Kolz (1993) documented that Wisconsin-ring dropper arrays project their fields somewhat further in a horizontal direction than similar-size spheres. Spheres, on the other hand, project their fields more evenly in all directions, including vertically towards the bottom and, perhaps less advantageously, upward to the water surface.

In addition to transfer of electrons, the process of electrolysis at the electrodes results in generation of gases and, more importantly, loss of metal ions from the anode to the water and deposition of metal ions from the water onto the cathode, usually as metallic oxides (Sharber, personal communication). Periodically, anodes may need to be replaced and cathodes cleaned (scraped or sanded) to recover lost surface area and performance (oxide coatings reduce electrode resistance). When electrodes are of the same size and type, some biologists periodically alternate their use as anodes or cathodes to reverse the buildup of metallic oxides (Sharber and Carothers, 1988), but the effectiveness of this procedure has not been reported.

Riddle (1984) suggested that it was not wise to buy aluminum punts (boats) second-hand from electrofishermen because the gauge of the metal might be substantially reduced. According to Sharber (personal communication), this is not a problem when a metal boat is used as the cathode. But when a metal boat is situated in an electric field and not used as an electrode, it has an intermediate electric charge, negative with respect to the anode and positive with respect to cathode. In this case, electrolytic reactions result in both formation of nonconductive metallic compounds on the boat's surface and loss of structural metal. Over time, the latter reaction can reduce the structural integrity of the boat. When a boat is used as a cathode, no metal is lost, but the nonconductive metallic compounds that form on the boat's surface can increase its electrical resistance. This coating can be scraped or sanded away periodically, but

in doing so, some structural metal may be inadvertently lost.

Results — Responses of Fish to Electric Fields

Movement toward an electrode in response to an electric field is not unique to aquatic vertebrates, or even organisms with nervous systems. Even individual cells respond. Halsband (1967) noted that common carp and trout erythrocytes placed in a powerful electric field (1,000 times more current density than used in electrofishing) first moved towards the anode (cataphoresis), then changed shape from oval to round, and finally disintegrated.

As in water, ionic conductivity is responsible for electric currents in blood and interstitial fluids of living tissues (Sternin et al., 1972, 1976), but transmission of electricity to and deep within the body of a fish is complex. Tissues and membranes have different and sometimes variable electrical qualities (e.g., conductivity, capacitance, and impedance–Sternin et al., 1972, 1976; Sharber et al., 1995). Skin, for example, is essentially resistive and dissipates much of the electrical energy as heat (perhaps some observed responses in fish are actually responses to heat). Some of the electrical energy that is transmitted across skin and other tissue membranes is reportedly transferred by capacitance. Presumably, with electrolytes on both sides of a membrane (e.g., water on one side of skin and interstitial fluids and blood in capillaries on the other side), the membrane functions somewhat as a dielectric in an electrical condenser and allows a momentary current across the membrane only as applied voltage is switched on, off, or suddenly increased or decreased. No current is transmitted by capacitance in PDC when the applied voltage is constant; therefore, the amount of charge transmitted by capacitance in PDC fields varies directly with frequency. But fish also exhibit very distinct, field-intensity dependent, responses under continuous DC. Direct electrical stimulation of afferent nerves probably also occurs through various external sensory structures in the skin, including the lateral-line canal system. Although not mentioned in literature reviewed for this report, the gills, which are the primary sites for ionic exchange, might also have a significant role in the transmission of electrical current to the blood and from there via the circulatory system to nerves and other tissues throughout the body.

Neurological responses to stimuli, nerve impulse transmission, and muscular actions in animals are electrochemical phenomena. In accord with the "all or none" principle of individual nerve response, each level of reaction requires a stimulus of a specific minimum intensity that must arrive quickly and be maintained for a minimum time. However, if a series of stimuli below the threshold level for nerve response are received over a sufficiently short period, their effect may be cumulative and still cause the nerve to respond according to the principle of temporal summation (Best and Taylor, 1943, as quoted by Haskell et al., 1954; Wydoski, 1980; Emery, 1984).

Biarritz and Bozeman Paradigms

In what has become known as the Biarritz paradigm, Blancheteau et al. (1961), Lamarque (1963, 1967a, 1990), Vibert (1963, 1967b), and Blancheteau (1967) developed a set of principles for nerve and muscle excitation in DC fields to explain the various responses of fishes observed in their experiments at the Biarritz Hydrobiological Station in France (Table 1). Lamarque (1967a) summarized these principles as follows:

"1. At a certain threshold, direct current initiates and maintains nerve or muscle excitation by the "autorhythm of excitation" (*see* Fessard 1936 and Monnier et al. 1940).
2. Short nerves in an electric field are excited at a higher value of current than long nerves (Laugier, 1921).
3. The greater the angle between a neurone in an electric field and the direction of current flow, the greater the current necessary to excite it (Fick, cited by Charbonnel-Salle 1881).
4. A neurone can only transmit its excitation to another neurone in the soma-axon direction.
5. The stimulus being produced by catelectrotonus at the cathode, an excitation can be conveyed to the next structure only if the cathode is on the soma side with regard to the axonic endings (normodromic stimuli).
6. Inversely, if the anode is on the soma side with regard to the axonic endings, the soma anelectrotonus can block a normodromic stimulus from another structure, and thus create an inhibition.
7. Nerve or muscle structures of a fish in an electric field can be excited or inhibited *in situ* since the fish body has itself become an electric field. According to the potential values, certain structures will be excited on account of their length (2), or their position (3); others will be inhibited (6), and yet others preserved from the action of current."

Lamarque (1967a) also noted that nerve interaction with PDC is further complicated by ". . . very complex physiological processes, such as chronaxies, spatial and temporal summations, synaptic delays, excitatory post-

Table 1. Reactions of fish in homogeneous fields of direct current. Star (★) indicates that the reaction was observed, em dash (–) that it was not observed, and blank that it was not studied. Modified from Table 1 in Lamarque (1967a).

V/cm[a]	Reactions[b]	Species[c]															
Fish facing anode		Ro	Sk	Ee	Ca	Gu	Te	Go	Br	Ra	Se	Bu	Su	Ti	Dr	Pl	So
	First reactions[d]			★	★	★	★	★	★	★	★			★	★		
0.10	Jerks of head		–	★				★	–	–	–	★		–	★	★	★
↓	Inhibition of swimming			★	★			★	★	★	★		★	★			
↓	Forced swimming[e]	★	–	★	★	★	★	★	★	★	★		★	–	★	–	–
↓	Galvanonarcosis	★		★	★	★	★	★	★	★	★	★	★	★	★		
↓	Protonos		★	★							★					★	★
↓	Bending of fins				★	★	★	★	★	★	★		★	★	★		
↓	Tetanus of maxillaries			★			★	★	★	★				★	★		
↓	Tetanus of gill covers				★	★	★	★	★	★				★	★		
↓	Quivering of tail, sagittal plane								★	★						★	★
↓	Pseudo-forced swimming			★					★	★				★			
↓	Tetanus of body, nervous origin			★					★	★							
↓	Opistotonos		★	★							–					★	★
1.25	Tetanus of body, muscular origin			★													
	Body pigmentation[f]			★				★	★	★				★			
Fish facing cathode		Ro	Sk	Ee	Ca	Gu	Te	Go	Br	Ra	Se	Bu	Su	Ti	Dr	Pl	So
0.10	First reaction[d]			★	★	★			★	★	★		★		★		
↓	Straightening of fins				★	★	★	★	★	★			★		★		
↓	Cathodic galvanotaxis		★	★				★	★	★	★			★	★	★	★
↓	Half turn towards anode			★	★	★	★	★	★	★	★		★	★			★
↓	Tetanus of body, nervous origin		★	★	★	★	★	★	★	★		★	★	★	★	★	★
↓	Maxillary spasms			★	★			★	★	★	★						
↓	Opistotonos		★	★					★	★	★				★	★	★
1.25	Tetanus of body, muscular origin			★													
	Discoloration of body[f]			★				★	★	★				★	★		
Fish first across field		Ro	Sk	Ee	Ca	Gu	Te	Go	Br	Ra	Se	Bu	Su	Ti	Dr	Pl	So
0.14	Temporary anodic curvature[d]		★	★	★	★		★	★	★			★	★		★	★
	Temporary cathodic curvature[d]			★					★	★							
0.35	Sustained anodic curvature		★	★	★	★	★	★	★	★			★	★	★	★	★
	Fin straightening on anode side, fin bending on cathode side					★			★	★							

[a]Approximate variation of voltage-gradient thresholds.

[b]Main reactions are underlined.

[c]Ro – roussette (Scyliorhinidae); Sk – skate (Rajidae); Ee – eel (*Anguilla anguilla*; Anguillidae); Ca – common carp (*Cyprinus carpio*; Cyprinidae); Gu – gudgeon (*Gobio gobio*; Cyprinidae); Te – tench (*Tinca tinca*; Cyprinidae); Go – golden fish (Cyprinidae ?); Br – brown trout (*Salmo trutta*; Salmonidae); Ra – rainbow trout (*Oncorhynchus mykiss*; Salmonidae); Se – seahorse (*Hippocampus* sp.; Syngnathidae); Bu – bullhead (*Cottus gobio*; Cottidae); Su – sunfish (*Lepomis* sp. ?; Centrarchidae); Ti – tilapia M (*Tilapia mossambica* ?; Cichlildae); Dr – dragonet (*Callionymus* sp. (Callionymidae); Pl – plaice (*Pleuronectes platessa*; Pleuronectidae); So – sole (*Solea vulgaris* ?; Soleidae).

[d]First reactions of fish facing anode; transient anodic curvature. These reactions occur only at closing the current. They are thus more concerned with interrupted current (PDC). By contrast, the "first reactions" of fish facing the cathode take place at the same threshold, no matter what the conditions of potential input are.

[e]Forced swimming. This reaction does not occur with flatfish, which just flatten themselves on the bottom of the tank. In the case of *Callionymus* and *Hippocampus*, this swimming is induced by pectoral or dorsal fins.

[f]Body pigmentation, discoloration. These reactions were not thoroughly studied.

synaptic potential . . ., polarity inversions due to openings of the circuit, etc." However, some of the concepts established by the Biarritz researchers are difficult to understand and have been questioned by other researchers (Hume, 1984; Sharber, personal communication).

In 1991 during an electrofishing-injury workshop in Bozeman, Montana, N.G. Sharber introduced another explanation for the responses of fish to an electric field. According to this theory, often referred to as the Bozeman paradigm, the observed responses of fish, including muscular seizures resulting in spinal and related injuries, are comparable to responses of humans and other animals subjected to electroconvulsive therapy and can be similarly explained as phases of epilepsy, specifically automatism, petit mal, and grand mal (Sharber and Black, 1999; Sharber et al., 1994, 1995; Sharber, personal communication).

How the underlying concepts of the Biarritz paradigm fit in the context of the Bozeman paradigm, and vice versa, has yet to be well explored. Because the phases of epilepsy are understood to be disorders of cerebral function, Sharber et al. (1994), and Sharber and Black (1999) suggested that the electric-field responses observed in fish are due to various levels of overstimulation of the central nervous system, either directly to the brain or short-circuited through the spinal cord. However, other researchers, including Haskell et al. (1954), Vibert (1963, 1967b), Lamarque (1967a, 1990), Edwards and Higgins (1973), and Wydoski (1980), concluded that the various responses elicited in fish by an electric field are the result of direct stimulation of not only the central nervous system, which controls voluntary reactions, but also the autonomic nervous system, which controls involuntary reactions, and muscles themselves. Haskell et al. (1954) and Lamarque (1967a, 1990) demonstrated that tetany in DC and muscular bends of the body toward the anode upon circuit closure in DC, or repeatedly in PDC, can be induced by direct overstimulation of efferent nerves or nerve endings associated with muscles. In those experiments, either efferent nerves were severed from the spinal cord, or the spinal cord was destroyed or removed prior to electric-field exposure. Muscular bends of the body often resulted in what was or would have been movement (taxis) towards the anode.

There is surely some truth to both paradigms, and perhaps a better understanding of the responses of fish to electric fields will require an integration of the two (possibly along with aspects of the power-transfer theory discussed below). The major intensity-dependent responses of fish described by both paradigms (reactive detection, undirected or inhibited swimming and taxis, and narcosis and tetany) are illustrated in Fig. 11 and discussed later in more detail. The electro-physiological mechanisms involved in epilepsy and electroconvulsive therapy might or might not be much better understood than those for the responses of fish to electric fields. In either case, a collaboration of biologists, including experts in neuro-physiology, should be fruitful for both disciplines. Certainly, the observed results of the Biarritz experiments and others mentioned above are valid under the conditions in which they were performed, but a much more complete and definitive understanding of the electrophysiological mechanisms involved is needed to better determine what electrical-field parameters and conditions will optimize desired electrofishing responses and minimize injury and other adverse effects.

Theory of Power Transfer from Water to Fish

Kolz and Reynolds (1989a) suggested that electrofishing should be viewed as a power-related phenomenon. More specifically, they hypothesized that the responses of fish to electric fields are directly related to the magnitude of power density (product of voltage gradient and current density) in the fish and that the in-fish power-density threshold for each response is constant (fixed) and independent of water conductivity. According to their theory of power transfer (Kolz, 1989a), when water conductivity (c_w) equals effective fish conductivity (c_f), 100% of the power density in the water is transferred to the fish (applied power density in the water, D_w, equals power density in the fish, D_f). But, as water conductivity either increases or decreases relative to the effective conductivity of the fish (conductivity mismatch), power transfer to the fish is progressively less efficient. To establish or maintain a desired level of power density in the fish under conditions of conductivity mismatch (perhaps just above the threshold for a specific response), power density in the water must be progressively increased beyond that of the match condition in accord with the relation $D_w/D_f = (1 + q)^2/(4q)$, where $q = c_w/c_f$ (the conductivity mismatch ratio; Kolz, 1989a). Subscript f represents effective in-fish values which match corresponding in-water values, subscript w, at the minimum of the curve represented by this equation.

When plotted on the log-log graph of power-density ratio versus water-conductivity ratio in Fig. 12, or the unique four-way log graph (Figs. 6 and 13) used by Kolz and Reynolds (1989b), the above relation yields what Kolz and Reynolds referred to as a normalized curve for predicting the increase in applied power-density needed to maintain a constant level of power-density in a fish (the curve minimum) as water conductivity changes. Note that the curve is symmetrical with a rounded bottom, like an

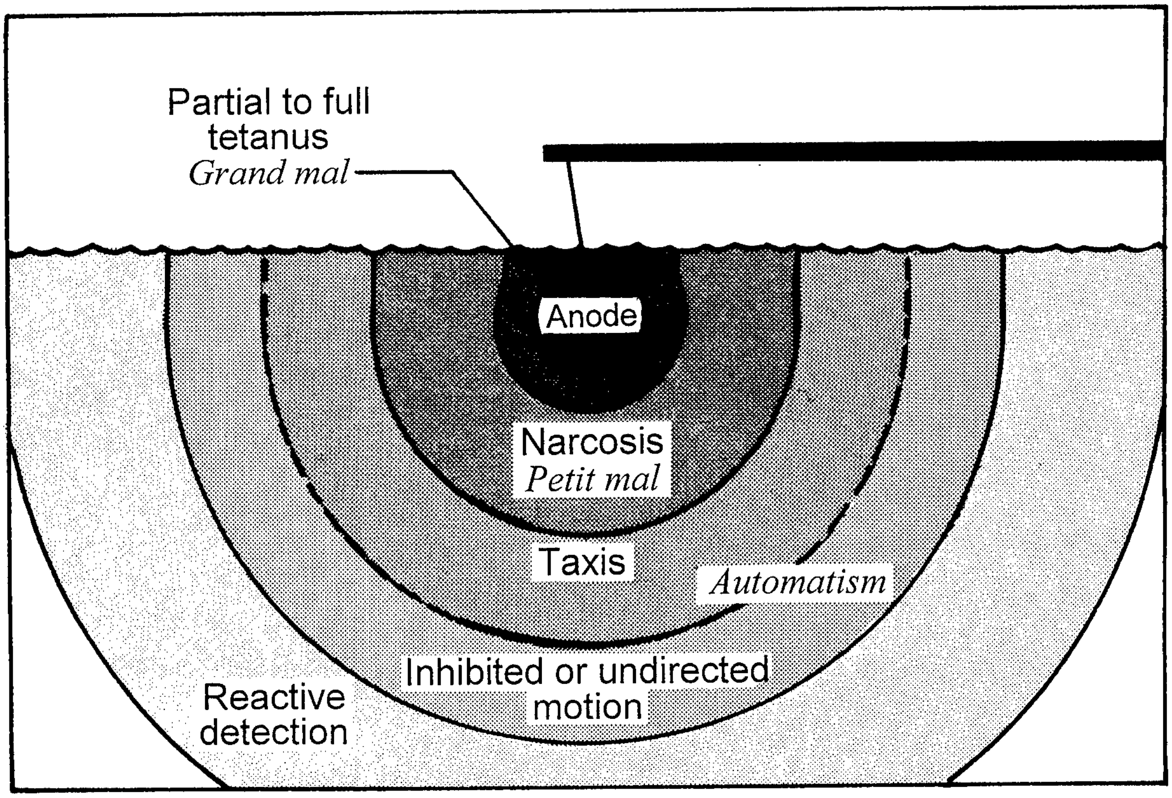

Fig. 11. Major intensity-dependent electrofishing response zones. (The outer boundaries of response zones for a spherical anode at the surface and sufficiently distant from the cathode are more-or-less hemispherical shells around the anode that represent field-intensity thresholds for the associated responses. Actual and relative sizes of the zones are specimen dependent (species, size, condition, and orientation) and vary with electrical output, electrode size and shape, and environmental conditions. Labels in italics represent corresponding phases of epilepsy as suggested by Sharber and Black, 1999, except that here the phase of tonic-clonic contractions (quivering or pseudo-forced swimming) between petit mal and grand mal (narcosis and tetany) is treated as the initial part of grand mal (partial tetany). Zones of taxis, narcosis, and tetany represent the effective range for fish capture using direct and pulsed direct currents.)

inverted normal curve, but with limbs that in the four-way enhancement of the graph (Figs. 6 and 13) become asymptotic to 45° lines to the left and right which respectively represent corresponding quantities of current density and voltage gradient. According to the theory, if such a curve fits in-water power-density threshold data for a specific response (as in Fig. 13) the coordinates at curve minimum represent the minimum in-water power density threshold, the fixed in-fish power-density threshold, the point at which 100% of the power density in the water is transferred to the fish, and the point at which water conductivity equals effective fish conductivity, all for that specific response. Hereafter in this report, the above relation and its corresponding curve are respectively referred to as the power-density-transfer equation and curve.

Although introduced a decade ago by Kolz and Reynolds (1989a) as a theory to be considered, further tested, and perhaps further developed and refined, the theory of power transfer has never been critically scrutinized in the literature for compliance with the laws of physics, electrical theory, or long-standing principles and theories regarding passage of electrical currents or charge to and through biological organisms or tissues. According to Kolz (personal communication), the theory has been substantiated using hard-wired techniques with dead fish and gelatins suspended in water, but his data have not yet been published. Nor have data beyond that presented by Kolz and Reynolds (1989b, 1990a) been generated to significantly support the theoretical relation between field-intensity response thresholds and the power-density-transfer equation and curve. Yet, the theory has been promoted as a critical concept for understanding and practicing electrofishing by the authors and instructors of the widely taught U.S. Fish and Wildlife Service course Principles and Techniques of Electrofishing (latest course

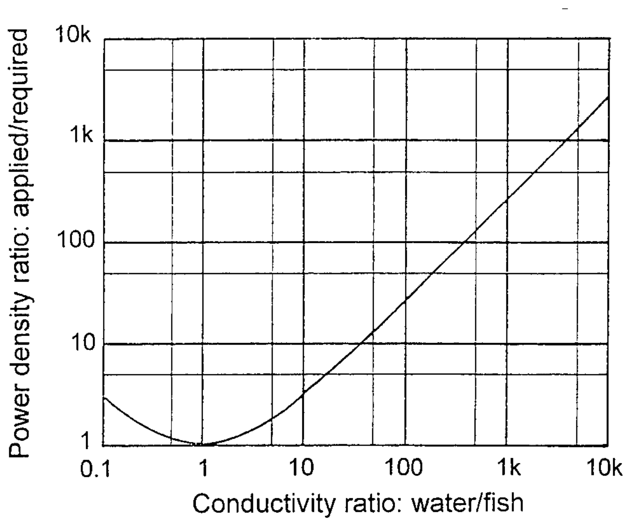

Fig. 12. Power-density-transfer curve. (Represents the relation $D_w/D_f = (1 + q)^2/(4q)$, where $q = c_w/c_f$ (the conductivity mismatch ratio, water to fish) for predicting the increase in applied power density in water (D_w) necessary to maintain a constant transfer of required power density (e.g., that for a desired response) to the fish (D_f) as the conductivity ratio (δ) increases or decreases from unity with changes in water conductivity. This relation was derived from concepts of normalized power and load mismatch by Kolz, 1989a and is fundamental to his theory of power transfer for electrofishing. Reproduced with permission from Fig. 1 in Kolz and Reynolds, 1989b; axis labels modified.)

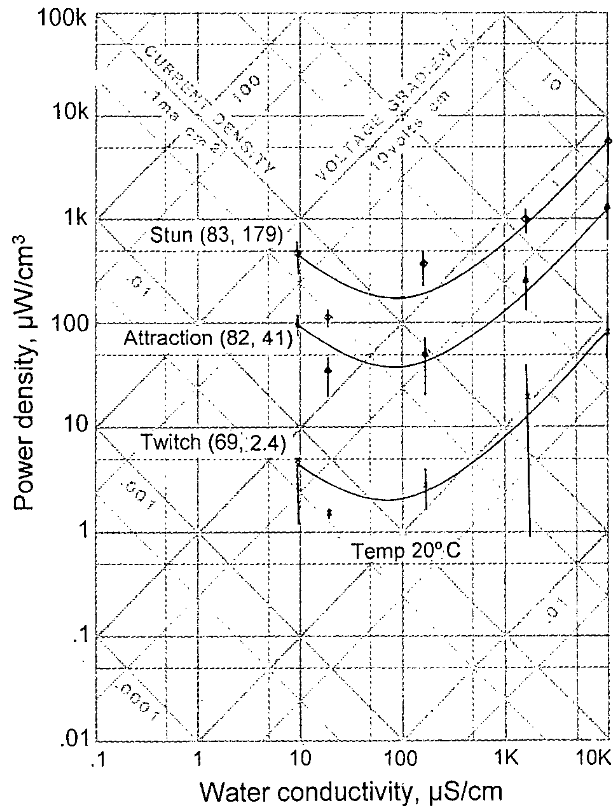

Fig. 13. Power-density-transfer curves fitted to peak-power-density threshold data for twitch, taxis (attraction), and narcosis (stun) in 6- to 9-cm-TL goldfish (*Carassius auratus*) subjected to homogeneous fields of DC. (Range and means of experimental data are represented by vertical bars and associated point symbols, respectively; ma = milliamperes or 1,000 microamperes. Reproduced with permission from Fig. 6 in Kolz and Reynolds, 1989b; axis labels modified.)

manual by Kolz et al., 1998) and by Reynolds (1996) in his chapter on electrofishing in the second edition of Fisheries Techniques (Murphy and Willis, 1996). Upon further development and testing, the theory or at least portions of it, might prove valid and useful, but questions regarding basic tenets remain.

Perhaps the first question to be asked is whether power itself is a quantity that can be transferred (or in part reflected as per some explanations of what happens under conditions of conductivity mismatch–Reynolds, 1995, 1996). Kolz (1989a) suggests in his text that electrical power is potential energy. However, in Kolz's (1989a) own glossary, and generally in physics textbooks, electrical power is technically defined as the rate of doing work or the amount of energy expended per unit time and power density as energy dissipated per unit time in a given volume of matter. As measures of expended or transformed energy, it follows that electrical power and power density cannot be transferred from water to fish (or anything else). According to Sharber (personal communication), only current (electrical charge conveyed per unit time by electrons or negative ions) is transferred in an electric field from water to fish, not power, and the amount of current transferred to and through the fish, or induced in it, is determined solely by the voltage gradient or differential across the tissues of the fish and the impedance of those tissues. Perhaps the differences in opinion are in part semantic, and the term "power transfer" should be replaced with "power induction" or a more appropriate term.

Possibly the earliest consideration of relationships among water resistivity (inverse of conductivity), fish resistivity, in-water power density, and in-fish power density in North American literature was that presented by Monan and Engstrom (1963). Although not considered further herein, a comparison between their theory and

mathematical derivations and Kolz and Reynolds' (1989a) theory of power transfer might be interesting and enlightening.

The response-threshold experiments by Kolz and Reynolds (1989b, 1990a) with 6- to 9-cm-TL goldfish appear to support at least the mathematical relationships of power-density theory. Using various currents (60-Hz AC; 50-Hz, square-wave PDC with 10, 25 and 50% duty cycles; and DC) across a range of water conductivities (~10, 100, 1,000, and 10,000 μS/cm), they determined the mean lowest peak-power densities at each conductivity required in water to initiate specific responses (thresholds for twitch, taxis, and stun). When plotted on log-log graphs relative to water conductivity (e.g., Fig. 13 for DC data), Kolz and Reynolds (1989b, 1990a) found that the response-threshold data for each tested response and current approximately fit the shape of their power-density-transfer curve. The data were fitted to the equation by nonlinear least squares regression, but some data, especially for DC as represented in Fig. 13, do not fit the power-density-transfer curve as well as others. Kolz and Reynolds (1989b) acknowledged the higher variability of their DC data and attributed it to inexperience in conducting their first set of experiments.

However, the position of these fitted power-density-transfer threshold curves, as defined by their minima (effective fish conductivities and fixed in-fish power-density thresholds), varied with each response and current tested. For example, they calculated that the effective conductivity of the goldfish for twitch was 69 μS/cm under DC, 83 to 99 μS/cm under PDCs, and 119 μS/cm under AC; for narcosis, the effective conductivity was 83 μS/cm under DC and 137 to 160 μS/cm under PDCs and AC. The existence of a different effective conductivity for each combination of response and current suggests that each response probably involved different tissues, electrical pathways, or physiological mechanisms. Otherwise, effective conductivities would be the same and threshold curves for each response would be vertically aligned. Although comparing across types of current, Kolz and Reynolds (1989b) particularly noted an increase in effective fish conductivity (averaged for all responses) relative to increasing pulse or current frequency (i.e., from 78 μS/cm for DC to 120 μS/cm for 50-Hz PDC to 138 μS/cm for 60-Hz AC) and suggested that it might be due to capacitive reactance. In-fish power density and effective fish conductivity probably also vary with species, size, condition, orientation in the field, and water temperature.

As Kolz and Reynolds (1989b) pointed out, effective fish conductivities based on the minima of power-density-transfer curves for specific responses in living fish are not the same as, and generally have much lower values than, fish conductivities determined by other methods. In their experiments, as discussed above, they reported mean effective conductivities of 69 to 160 μS/cm for goldfish depending on the specific response observed and current tested. In contrast, Monan and Engstrom (1963) reported fish conductivities of 505 to 1,266 μS/cm for sockeye salmon, Sternin et al. (1972, 1976) reported a range of conductivities from 319 to 3,571 μS/cm for a variety of freshwater fishes, and Haskell (1954) reported an approximate conductivity of 667 μS/cm (resistivity of 1,500 ohm-cm) for the flesh of brown trout. Haskell (1954) considered effective resistivity of the fish (inverse of conductivity) to be equal to water resistivity when a fish or its flesh failed to distort the distribution of voltage or voltage gradient around it (Fig. 10) when placed in a homogeneous field in a long, narrow trough.

Congruence of a single set of experimental response-threshold data with Kolz's (1989a) power-density-transfer curve does not necessarily validate that mathematical relation, much less the underlying concepts of power-transfer theory as presented by Kolz and Reynolds (1989a). Comparable response-threshold evidence based on other species and independently replicated tests of goldfish are needed. Despite an attempt by Jesien and Hocutt (1990) and implications by Fisher and Brown (1993), no comparable data have been reported in the literature to further support or disprove the theory of power transfer.

Jesien and Hocutt (1990) determined in-water field-intensity thresholds for 50% tetany in 18- to 22-cm channel catfish exposed for 1 s to 30-Hz and 120-Hz PDCs and two pulsed ACs in water conductivities of 100, 1,000, and 10,000 μS/cm at 20° C. However, they needed at least one more set of trials at a lower water conductivity to demonstrate congruence with or divergence from the normalized curve predicted by power-transfer theory. Depending on the type of current and fish orientation upon exposure under the PDCs (towards anode or cathode), peak voltage-gradient thresholds ranged from 0.22 to 0.37 V/cm at 100 μS/cm, 0.12 to 0.29 V/cm at 1,000 μS/cm, and 0.09 to 0.23 V/cm at 10,000 μS/cm; corresponding peak power densities were 4.8 to 13.4, 14.4 to 84.1, and 81 to 515 $\mu W/cm^3$. Voltage gradients decreased and power densities increased progressively with increasing water conductivity for all but one current, waveform, and fish-orientation combination (threshold voltage gradient for the response was lowest at 1,000 μS/cm for 30-Hz PDC with fish facing anode). No in-water, power-density, threshold minima were apparent in or calculated for the data.

In a personal communication reported by Jesien and Hocutt (1990), A. Kolz suggested that the power-density minima and corresponding effective fish conductivities for the fish response tested in each of their treatments probably occurred at slightly lower water conductivities than tested. However, if Jesien and Hocutt's data conform to Kolz's (1989a) power-density-transfer curves, the curve

minima for at least some treatments might have occurred at a water conductivity (and effective fish conductivity) somewhat above 100 μS/cm with the value at 100 μS/cm being on the left upside portion of the curve. This possibility can be explored by assuming that the experimentally derived threshold values at the three conductivities tested for each treatment do fit a power-density-transfer curve and calculating the fixed in-fish power density (D_f) and effective fish conductivity (c_f) for each curve (the coordinates of the curve minimum) based on any two data points presumably on the respective curve. The coordinates for the minimum of each curve can be calculated by: (1) rearranging the power-density-transfer equation given in the first paragraph of this section to solve for D_f and setting the resulting equations for the coordinates of each of any two data points on the curve equal to each other [$D_f = 4D_{w1}(c_{w1}/c_f)/(1 + (c_{w1}/c_f))^2 = 4D_{w2}(c_{w2}/c_f)/(1 + (c_{w2}/c_f))^2$]; (2) solving for c_f; and (3) substituting the value of c_f back into the power-density-transfer equation for either data point to determine the value of D_f. Doing so using threshold approximations for the 120-Hz-PDC, fish-facing-cathode treatment at 100 and 10,000 μS/cm (approximately 5 and 100 $\mu W_p/cm^3$, respectively), the calculated minimum coordinates would be an effective fish conductivity of 126 μS/cm at an in-fish power-density threshold of 4.9 $\mu W/cm^3$. For threshold approximations at 100 and 1,000 μS/cm (14.4 $\mu W/cm^3$) and at 1,000 and 10,000 μS/cm, the calculated minimum coordinates would be 106 μS/cm at 5.0 $\mu W/cm^3$ and 227 μS/cm at 8.7 $\mu W/cm^3$, respectively. For whatever reason (perhaps inadequate or imprecise data), these results do not bode well for the fit of all three data points on the power-density-threshold curve. A similar extrapolation of coordinates for threshold-curve minima for Jesien and Hocutt's (1990) other treatments might prove interesting, but would probably also be inadequate to support or disprove application of the mathematical relations of power-transfer theory to fish.

Fisher and Brown (1993) conducted a series of caged-fish experiments with "prepositioned areal" electrofishing gear to determine effective distances from the electrodes for 100% immobilization of fishes in streams of varying conductivity. Each cage contained a mixed assemblage of locally caught species. With measurements made from the center of cages set at various distances from the electrodes, Fisher and Brown (1993) reported that the average peak-field intensities for cages farthest from the electrodes with 100% of the fish immobilized (very coarse threshold approximations) were 237 $\mu W_p/cm^3$ in a 35-μS/cm stream, 10 $\mu W/cm^3$ in a 60-μS/cm stream, 77 $\mu W/cm^3$ in a 120-μS/cm stream, and 80 $\mu W/cm^3$ in a 125-μS/cm stream. Because a plot of the mean threshold values relative to water conductivity was V-shaped (lowest value at the intermediate water conductivity) and fit between Kolz and Reynold's (1989b, 1990a) goldfish threshold curves for twitch and stun under AC, Fisher and Brown (1993) suggested that the results were congruent with power-transfer theory. However, if those data are plotted on a log-log graph like those used by Kolz and Reynolds (1989b, 1990a; e.g., Fig. 13), it is obvious that the resulting curve is much too tight (left and right limbs too steep) to approximate Kolz's (1989a) normalized power-density-transfer curve. Also, unlike Jesien and Hocutt's (1990) data above, no combination of pairs of data points including the power-density value for the 60-μS/cm stream can be made to approximate the normalized threshold curve (calculations result in negative values for effective fish conductivities and threshold minima). Using data points for the 35 and 120 or 125 μS/cm streams, calculated minimum coordinates for fitted power-density curves are 1,499 μS/cm at 21 $\mu W/cm^3$, or 884 μS/cm at 35 $\mu W/cm^3$, respectively. Fisher and Brown's (1993) data certainly do not approximate a power-transfer curve, nor were their field experiments designed or intended to test the mathematical relations of power-transfer theory; experiments to that end need to be much more precise and controlled.

Ten years after Kolz and Reynolds (1989a) proposed their theory of power transfer in fish, I found only two published accounts of practical field applications. Burkhardt and Gutreuter (1995) described a procedure by which aspects of the power-transfer theory were used to standardize electric fields in a major long-term monitoring program using 60-Hz PDC (25% duty cycle) in waters with conductivities ranging from 250 to 700 μS/cm and water temperatures from 15 to 35° C. Chick et al. (1999) adopted the procedure to evaluate use of airboat electrofishing with 60 or 120-Hz PDC for sampling large fishes in shallow, vegetated habitats with water conductivities of about 200 to 950 μS/cm and temperatures of 15 to 25° C. The procedure consists of preparing a table of peak-power-output goals for the anticipated range of water conductivities and temperatures, then using that table to adjust electrical output for measured water conductivity and temperature with the expectation that the resulting distribution of power densities in the water will cause comparable responses (e.g., narcosis) by fish of the same species and size at the same relative position (distance from an anode) during each sampling effort. The tables for each study were based on electrical and physical parameters recorded for the most successful (presumably highest catch-per-unit-effort) unstandardized collections taken earlier in each program and an effective-fish-conductivity value of 150 μS/cm. The latter value was selected from the upper end of the range of effective conductivities reported by Kolz and Reynolds (1989b, 1990a) for goldfish subjected to a waveform and duty cycle similar to that used by Burkhardt and Gutreuter (1995).

However, for standardizing electrofishing operations in waters with similar ranges of conductivities and temperatures, perhaps the procedures used by Burkhardt and Gutreuter (1995) and Chick et al. (1999) are more complex than they need to be; a direct in-water, voltage-gradient-measurement approach might be simpler, just as effective, and more certain. With this approach, electrical output would be adjusted at the beginning of each sampling effort (and again whenever conductivity and temperature are likely to differ significantly) until a target voltage gradient is measured at a standardized position in the electric field (e.g., 1 m from an anode towards the boat). Based on Kolz and Reynolds' (1989b, 1990a) experiments (Fig. 14), voltage-gradient response thresholds for water conductivities beyond 200 µS/cm, and especially 500 µS/cm, decrease so gradually with increasing water conductivity (about 0.7 to 0.5 V/cm for the stun threshold in 6- to 9-cm-TL goldfish using a current comparable to that used by Burkardt and Gutreuter, 1995) that one value (e.g., 0.6 V/cm) could be effectively used as the target voltage gradient for standardization over the full range of conductivities encountered in the above discussed investigations.

For a little more precision when using the in-water-measurement approach for standardizing electrofishing fields or when working in lower conductivity waters, voltage-gradient thresholds for the desired response and current using the goldfish model could be read directly from a portion of the appropriate Kolz and Reynolds' (1989b, 1990a) graph enlarged for the conductivity range of interest. Alternatively, a comparable curve of in-water voltage-gradient thresholds (E_w) versus water conductivity (c_w) could be generated by using the equation $E_w = E_f \times (1 + (c_f / c_w))/2)$ with the voltage gradient (E_f) and water conductivity (c_f) values corresponding to the power-density minimum for the pertinent power-density-transfer threshold curve by Kolz and Reynolds (e.g., Fig. 14; the referenced equation is derived from the power-density-transfer equation based on the definition of power density, $D = cE^2$). Of course, these suggestions assume that the mathematical relations of the power-density theory are valid and that Kolz and Reynolds' (1989b, 1990a) data for goldfish and the electrical currents tested are suitable models for the targeted fish and electrofishing operation.

Voltage-gradient and power-density threshold curves based on Kolz and Reynolds' (1989b, 1990a) goldfish data for narcosis (e.g., stun in Fig. 13 for DC) are compared relative to water conductivity for each tested current in Figs. 14 and 15, respectively. Upper and lower graphs in each figure are the same except that the upper graphs use unequal logarithmic scales and the lower graphs use arithmetic scales for the more limited range of freshwater conductivity. Regardless of whether field intensity is represented by units of voltage gradient or power density, threshold curves for narcosis in these graphs are similar for AC and the three PDCs but notably higher for DC at moderate to high conductivities (about 60% higher among voltage gradient curves). Comparable reactive detection (twitch) curves would be similar for each of the currents (Kolz and Reynolds, 1989b, 1990a). As suggested above, beyond water conductivities of 250 µS/cm, and especially beyond 500 µS/cm, voltage-gradient thresholds decrease so gradually that one approximate value (for each species, size range, water temperature, and waveform) can effectively approximate the threshold for a particular response at all higher levels of conductivity in fresh water (Fig. 14). For moderate to high water conductivities, corresponding in-water power-density or current-density thresholds would increase significantly with increasing water conductivity (Fig. 15).

Despite possible problems with semantics and technical aspects of the power-transfer theory (including the concept implied by its name) and apparent support by just one set of threshold data for one species, the mathematical relations of the theory appear to be valid and useful at least for defining or predicting field-intensity threshold curves for selected responses over a wide range of water conductivities. Aside from this and the standardizing procedure described by Burkhardt and Gutreuter (1995), the utility of in-fish power-density response thresholds and effective fish conductivities in electrofishing operations has not yet been realized. Until such utility is realized, response-threshold data are probably more easily understood and used in terms of peak-voltage gradients, which, unlike power density, can be measured directly in the water. Also, power-density can only be determined by calculation from measurements of voltage gradient and water conductivity, and for use in the field, including standardization of electric fields based on in-water measurements, it must be converted back to voltage gradient. Accordingly, most field-intensity data in the remainder of this review, including response thresholds, are presented as voltage gradients (when water conductivity data are also available, corresponding current density and power density values can be calculated).

Major Intensity-Dependent Responses

The sequence of generally observed, intensity-dependent responses by fish as they approach the anode in an electrofishing field are illustrated in Fig. 11. Except for their relation to epileptic responses and the distinction between narcosis and tetany (an important distinction overlooked in much of the literature), most of these responses were documented as early as the 1920's (e.g., Scheminzky, 1924, according to Lamarque, 1990). Vibert (1963) and his associates at the Biarritz Station found that not all fishes exhibited the same set of responses in

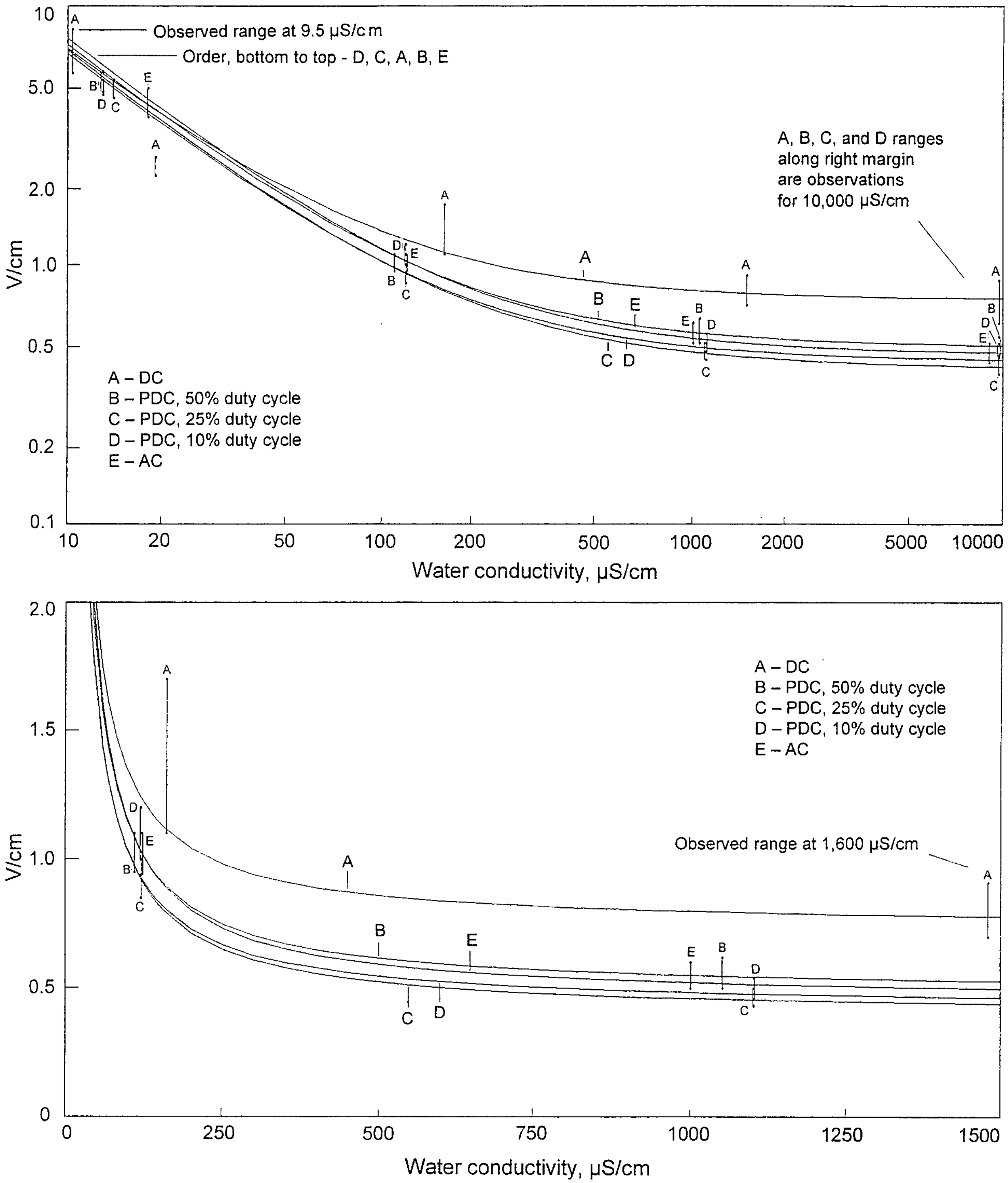

Fig. 14. Peak-voltage-gradient-threshold curves for narcosis (stun) of 6- to 9-cm-TL goldfish (*Carassius auratus*) in homogeneous fields of DC; 50-Hz, square-wave PDC with duty cycles of 50%, 25%, and 10%; and 60-Hz sinusoidal AC. (These in-water curves are an alternative representation of the power-density-transfer curves for narcosis in Figs. 6–10 of Kolz and Reynolds, 1989b. The vertical ranges denoted by small capital letters and associated with each curve approximate the corresponding ranges of experimental threshold data provided in Kolz and Reynolds' graphs.)

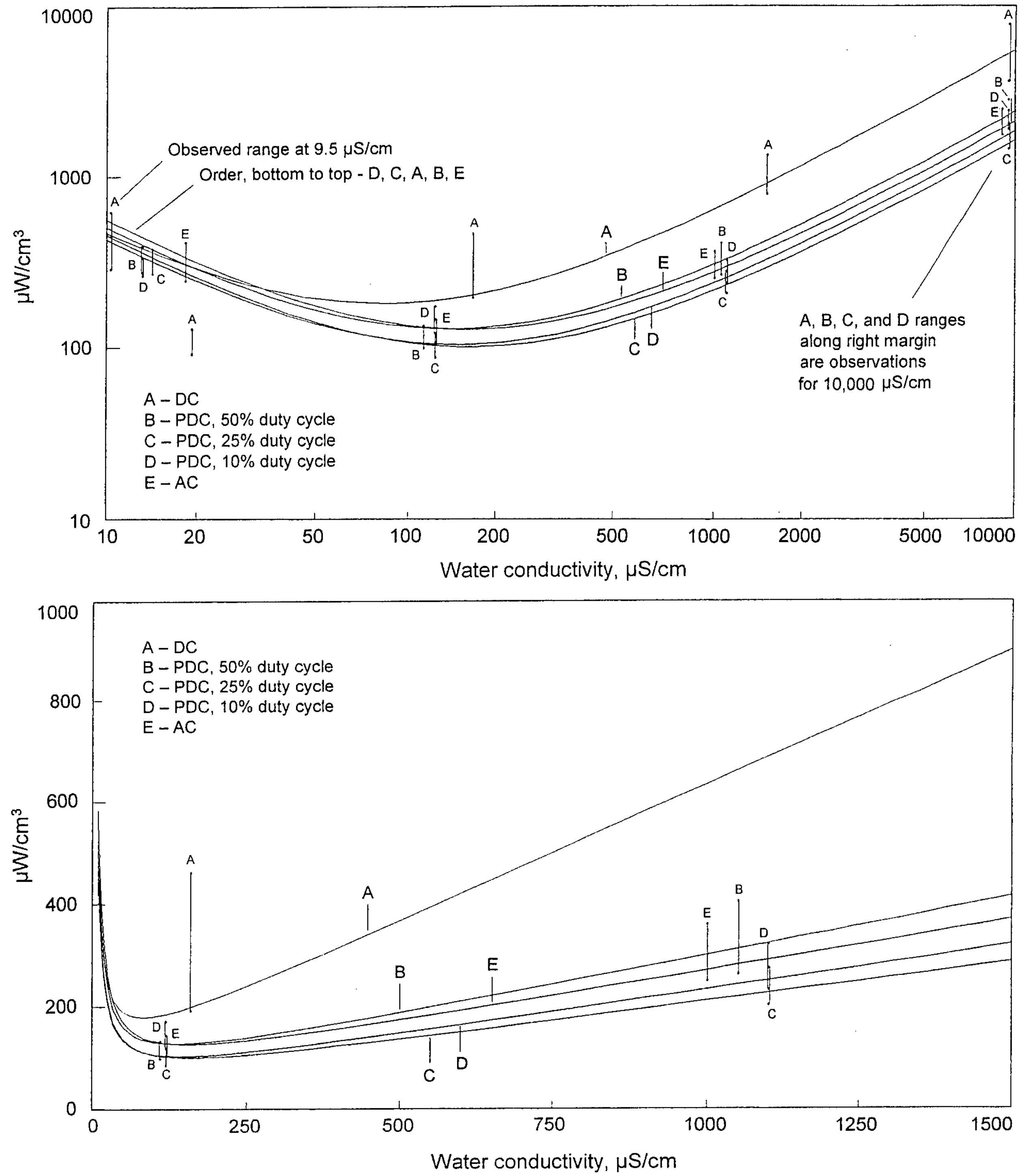

Fig. 15. Peak-power-density-threshold curves for narcosis (stun) of 6- to 9-cm-TL goldfish (*Carassius auratus*) in homogeneous fields of DC; 50-Hz, square-wave PDC with duty cycles of 50%, 25%, and 10%; and 60-Hz sinusoidal AC. (These in-water curves are an alternative representation of the power-density-transfer curves for narcosis in Figs. 6–10 of Kolz and Reynolds, 1989b. The vertical ranges denoted by small capital letters and associated with each curve approximate the corresponding ranges of experimental threshold data provided in Kolz and Reynolds' graphs.)

DC that they observed for brown trout and European eel (Table 1). Vibert (1963) suggested that there is "... a sort of competition between the reaction to the particular electric stimulus and the general behavioral response to normal ecological stimuli." Biarritz biologists also reported that some responses differed with the type of current. Lamarque (1990) specifically warned that, because of the dynamic behavior and unlimited types of PDC available, responses of fish in PDC can be quite different from those in DC and that confusion between them would lead to a considerable misunderstanding of electrofishing procedures.

Based on either laboratory or field observations, other biologists reported results that contradict the Biarritz observations and sometimes each other. For example, in PDC fields with a sufficient range of voltage gradients to bound response thresholds, the Biarritz researchers observed anodic taxis (and tetany) in trout (brown or rainbow) and European eels but no narcosis (100 Hz, 1-ms pulses). Conversely, Kolz and Reynolds (1989b), in experiments with goldfish, observed narcosis but no taxis (50 Hz; 2, 5, and 10-ms pulses). Yet, in practical electrofishing operations, it is the strength and range of both responses, taxis and narcosis, that generally make PDC so useful. Contrary to the findings of Kolz and Reynolds (1989b), Bird and Cowx (1993) documented both taxis and narcosis in goldfish under a variety of PDC waveforms and frequencies (30 to 600-Hz square, 50-Hz quarter-sine, 50-Hz exponential; pulse widths 0.2–30 ms). Taxis towards the anode is the forte of electrofishing with DC, but Haskell et al. (1954) reported that, even under uniform laboratory conditions, the response was very erratic; certain individuals were quickly drawn to the anode, but others exhibited only partial or no taxis. Kolz (personal communication) noted that participants in the U.S. Fish and Wildlife Service electrofishing course have reported that taxis may or may not occur in PDC fields (species not specified, presumably field observations). Meismer (1999) compared responses and response thresholds for Colorado pikeminnow and rainbow trout in homogeneous fields of DC, 15- or 60-Hz, square-wave PDC, or CPS, and reported that both species exhibited expected classical responses in all currents. However, in both species, CPS caused more of a shudder than a sharp twitch as observed with other currents. Also, taxis was notably strongest in DC and not quite as strong in CPS as in simple PDCs, and when current was switched off, fish recovered more quickly from DC than other currents tested. Despite these reports of variable and contradictory responses, Sharber and Black (1999) suggested that although the threshold levels for and intensity of the various responses might differ, the general responses of fish to an electric field are essentially the same regardless of whether AC, DC, or PDC is used.

The responses indicated in Fig. 11 are those expected of fish in DC and possibly all electric fields when facing the anode (or either electrode in AC). According to the Biarritz paradigm, responses and thresholds differ when fish face the cathode or are perpendicular to the lines of current (Table 1). Jesien and Hocutt (1990) found that channel catfish in homogeneous PDC fields are more sensitive to tetany when facing the cathode than when facing the anode. Changes in other environmental or experimental conditions may also affect fish responses. The Biarritz and most other experiments mentioned above were conducted in homogeneous fields. Whether responses or thresholds specific to fish facing in either direction (toward the anode or cathode) would differ in a heterogeneous field might depend on whether the fish are closer to the anode or the cathode (the matter was not addressed in literature reviewed for this report). Vibert (1963) and Northrop (1967) noted that under field conditions it is impossible to distinguish each of the responses documented in laboratory experiments, especially in flowing water or a moving field wherein fish are continually reoriented relative to the lines of current and can be moved quickly from one response zone to another.

Response Thresholds

Electrofishing fields are nearly always heterogeneous, with field intensity highest at the electrode surface and decreasing geometrically from that surface to barely perceptible levels a few meters away. The outer boundary for each response zone illustrated in Fig. 11 represents the minimum in-water field intensity (i.e., voltage-gradient, current-density, or power-density) or threshold for that response. The specific values for these thresholds vary with water conductivity and temperature, electric-field waveform and frequency, and the pertinent electrical and physiological characteristics of the fish, which, considered as a whole, define its effective conductivity. According to Whitney and Pierce (1957), Halsband (1967), and Emery (1984), the electrical conductivity of a fish (not necessarily its effective conductivity) depends on its species, size, shape, condition, surface area, and possibly even the size of its scales.

Response zones shrink or expand for individual fish according to their orientation in the field. As suggested above and in Table 1, both response threshold and nature of response can vary with orientation. A fish in taxis when facing the anode might at the same location be only in the zone of reactive detection when oriented perpendicular to lines of current. In the latter situation, the fish would retain voluntary control of its movements and could dart sufficiently away to escape further influence by the field. If the fish turns from the perpendicular position instead of darting directly away, the voltage differential across

the fish (from head to tail) would increase until at some point the fish loses voluntary control and enters a state of automatism. The fish might then remain in this state or, through random movement and changes in orientation, return to the zone of reactive detection or possibly begin anodic taxis. Most fish in a state of anodic taxis continue in this state until they reach the zone of narcosis. Momentum from taxis or drift can sometimes carry a fish from the zone of narcosis into the zone of tetany near the anode. In experimental homogeneous fields, Edwards and Higgins (1973) occasionally observed fish passing into and out of a state of paralysis (stun) as their orientation changed relative to the lines of flux. They also noted that, when homogeneous field intensity was not sufficient to stun, fish which could not escape or move to less-intense zones tended to align themselves perpendicular to the lines of flux (parallel to isopotential planes), where total voltage across their bodies was least. Even when all factors noted above as affecting response thresholds are the same, including orientation, observed threshold values apparently vary somewhat with individual specimens and probably even in repeated tests of the same individual with or without adequate stress-recovery periods between tests.

For specific species, size ranges, and other conditions, in-water field-intensity thresholds can be approximated for various responses by fish and used to define effective electrofishing fields. In-water, peak-voltage-gradient threshold data by species, water conductivity, and current type for twitch (reactive detection), anodic taxis, and narcosis (or stun) are summarized from selected references in Table 2. However, data in Table 2 from Sternin et al.'s (1976) Appendix 4 are summarized across species and may include mean (PDC) or rms (AC) voltage-gradient thresholds. The term stun covers both narcosis and tetany, which may be difficult to distinguish. Some stun threshold data from Sternin et al. (1976) might actually be the threshold for loss of equilibrium prior to narcosis. All known threshold data for endangered cypriniform fishes from the Colorado River Basin (Ruppert and Muth, 1997; Meismer, 1999) are included in Table 2. Some relative response-threshold data is also provided in Table 1.

Most experiments to determine field-intensity thresholds for specific responses by fish are conducted in homogeneous fields. However, one set of threshold experiments by Taube (1992) was uniquely conducted in premapped heterogeneous fields to better simulate electrofishing conditions in the field. The results were extremely wide ranges for twitch and narcosis thresholds with unexpectedly high means but minima comparable to thresholds determined by Taube (1992) and most other investigators using homogeneous fields in the same range of water conductivity (Table 2). Whether the unusually wide and high ranges of threshold values from Taube's (1992) heterogeneous-field experiments are artifacts of experimental methodology or reflect a real difference between response thresholds in the two types of electric fields is a matter that deserves further investigation.

As noted earlier, Kolz and Reynolds (1989b) suggested that peak-intensity threshold values for AC and PDC are probably more biologically significant than mean-intensity values. This suggestion was based on their observation that across all tested waveforms, the ranges of power-density-curve minima for the thresholds of each response in goldfish were much narrower (values more similar) using peak rather than mean field-intensity data. For example, using corrected data for twitch threshold curves from Table 1 in Kolz and Reynolds (1989b), the range of peak field-intensity minima, 0.13–0.19 V_p/cm (2.1–2.7 $\mu W_p/cm^3$), is much narrower than that for mean field-intensity minima, 0.015–0.19 V_m/cm (0.023–2.4 $\mu W_m/cm^3$). Matching water and effective fish conductivities at those curve minima were 69–119 µS/cm). Mean (effective) power-density minima for 50%, 25%, and 10% (duty cycle) PDC in Kolz and Reynolds' (1989b) Table 1 were miscalculated; respective corrected minima are 0.68, 0.17, and 0.023 $\mu W/cm^3$ (rather than 1.4, 0.7, and 0.2 $\mu W/cm^3$) for twitch and 32, 6.3, and 1.0 $\mu W/cm^3$ (rather than 64, 25, and 10 $\mu W/cm^3$) for stun. Voltage-gradient threshold data for AC and PDC discussed earlier from Edwards and Higgins (1973) and that summarized in Table 2 (except possibly data from Sternin et al., 1976) represent peak field intensities.

Typical voltage-gradient response thresholds reported for fish in fresh waters of moderate to high conductivity range from about 0.01 to 0.1 V/cm for twitch to about 0.5 to 1.5 V/cm for tetany (Vibert, 1963; Lamarque, 1967a, 1990; Sternin et al., 1972, 1976; Kolz and Reynolds, 1989b, 1990a; Bird and Cowx, 1993; Ruppert and Muth, 1997). However, the range for a particularly sensitive species can be much lower. Jesien and Hocutt (1990) found this to be the case for channel catfish tested at water conductivities of 100, 1,000, and 10,000 µS/cm; voltage gradient thresholds for 50% tetany ranged from 0.1 to 0.4 V/cm. For water conductivities greater than 100 µS/cm, Reynolds (1996) concluded that voltage gradients of 0.1 to 1.0 V/cm are generally effective for inducing narcosis (and possibly tetany) in most species.

However, in low conductivity waters, voltage-gradient thresholds can be much higher than the typical figures noted above. In water of just 4 µS/cm (16–18° C), Bird and Cowx (1993) reported twitch thresholds of 1.4 to 3.0 V_p/cm for juvenile rainbow trout ($\bar{x}$ = 14 cm) subjected to a variety of PDCs, but at 1,000 µS/cm, even narcosis thresholds for respective currents were much lower, ranging from 0.5 to 1.8 V_p/cm. As summarized in Table 2, thresholds in waters with conductivities between 9 and

Table 2. In-water, peak-voltage-gradient (V/cm) response thresholds by fish species, water conductivity, and type of electrical current. Summarized from selected literature.[a]

Source, species, length conductivity, temperature Current[d]	Response threshold, peak V/cm[b] Twitch Mean	Twitch Range	Anodic taxis Mean	Anodic taxis Range	Narcosis or stun[c] Mean	Narcosis or stun[c] Range
Sternin et al. (1976), all species and lengths combined from various studies						
20 µS/cm, (no temperature data)						
DC	(no data)	0.28–0.32[e]	(no data)			
50 to 100 µS/cm, 2 to 13° C (+?)						
DC	0.29[f]	0.1–0.62	0.94	0.25–2.0	2.1[f]	0.99–2.8
AC (50, 60 Hz)	0.04[f]	0.01–0.06	(not applicable)		0.13[f]	0.10–0.19
143 to 160 µS/cm, 0.2 to 18°C						
AC (50, 60 Hz)	0.03[f]	0.02–0.04	(not applicable)		0.12[f]	0.08–0.41
174 to 286 µS/cm, 4 to 21°C						
DC	(no data)	0.25[e]	(no data)			
PDC (5, 10, 15 Hz)	0.13[f]	0.06–0.30	0.35[f]	0.10–0.71	1.4[f]	0.30–4.4
AC (50, 60 Hz)	0.04[f]	0.01–0.06	(not applicable)		0.21[f]	0.05–1.1
300 to 740 µS/cm, 2 to 16° C (+?)						
DC	0.07[f]	0.01–0.14	0.23[f]	0.08–0.66	0.51[f]	0.22–0.82
PDC (5, 10, 15 Hz)	0.06[f]	0.06–0.10	0.15[f]	0.10–0.21	0.37[f]	0.30–0.53
AC (50, 60 Hz)	0.03[f]	0.01–0.06	(not applicable)		0.15[f]	0.04–0.47
880 to 2,000 µS/cm, (no temperature data)						
DC	(no data)	0.24[d,e]	0.22–0.27		(no data)	
AC (50, 60 Hz)	0.02[f]	0.01–0.03	(not applicable)		0.09[f]	0.07–0.14
≥10,000 µS/cm (saltwater, brackish and marine), 7 to 30°C						
DC	0.02[f]	0.01–0.04	0.11[f]	0.04–0.20	0.28[f]	0.11–0.50
PDC (4–500 Hz)	0.07[f]	0.03–0.14	0.20[f]	0.06–1.0	0.45[f]	0.13–0.82
AC (50 Hz)	0.02[e]		(not applicable)		0.12[e]	
Kolz and Reynolds (1989b), goldfish (*Carassius auratus*), 6 to 9 cm TL[g]						
9 to 19 µS/cm, 20°C						
DC	0.52	0.26–0.76	2.4	1.1–3.6	4.9	2.2–8.1
PDC (50 Hz, 10%)	0.60	0.42–0.69	(not observed)		4.8	4.5–5.1
PDC (50 Hz, 25%)	0.60	0.45–0.65	(not observed)		4.8	4.4–5.2
PDC (50 Hz, 50%)	0.60	0.55–0.68	(not observed)		5.1	4.6–5.5
AC (60 Hz)	0.50	0.40–0.55	(not applicable)		4.5	3.7–4.8
110 to 160 µS/cm, 20°C						
DC	0.12	0.10–0.15	0.56	0.35–0.67	1.5	1.1–1.7
PDC (50 Hz, 10%)	0.16	0.13–0.18	(not observed)		1.1	1.0–1.2
PDC (50 Hz, 25%)	0.17	0.13–0.20	(not observed)		0.95	0.85–1.00
PDC (50 Hz, 50%)	0.17	0.10–0.22	(not observed)		1.05	0.95–1.10
AC (60 Hz)	0.10	0.06–0.14	(not applicable)		1.00	0.94–1.10
1,000 to 1,600 µS/cm, 20°C						
DC	0.11	0.02–0.15	0.40	0.29–0.46	0.85	0.70–0.91
PDC (50 Hz, 10%)	0.10	0.08–0.11	(not observed)		0.49	0.46–0.54
PDC (50 Hz, 25%)	0.09	0.07–0.10	(not observed)		0.46	0.43–0.50
PDC (50 Hz, 50%)	0.10	0.09–0.11	(not observed)		0.58	0.50–0.62
AC (60 Hz)	0.08	0.06–0.09	(not applicable)		0.55	0.50–0.60

Table 2. Continued.

Source, species, length conductivity, temperature Current[d]	Response threshold, peak V/cm[b] Twitch Mean	Twitch Range	Anodic taxis Mean	Anodic taxis Range	Narcosis or stun[c] Mean	Narcosis or stun[c] Range
9,700 to 10,000 μS/cm, 20°C						
DC	0.09	0.08–0.11	0.37	0.25–0.42	0.80	0.60–0.88
PDC (50 Hz, 10%)	0.08	0.07–0.09	(not observed)		0.47	0.44–0.50
PDC (50 Hz, 25%)	0.10	0.07–0.11	(not observed)		0.40	0.38–0.45
PDC (50 Hz, 50%)	0.08	0.08–0.09	(not observed)		0.48	0.45–0.53
AC (60 Hz)	0.07	0.06–0.08	(not applicable)		0.45	0.42–0.50
Taube (1992), rainbow trout (*Oncorhynchus mykiss*), 31 to 48 cm FL[h]						
103 μS/cm, 11°C						
DC	0.37	0.18–0.56	(no data)		4.4	0.44–6.4
PDC (20 Hz, 25%)	0.30	0.19–0.43	(no data)		2.3	0.47–5.0
PDC (20 Hz, 75%)	0.28	0.15–0.50	(no data)		3.1	0.53–10.4
PDC (30 Hz, 50%)	0.36	0.15–0.71	(no data)		3.6	0.92–6.5
PDC (60 Hz, 50%)	0.35	0.11–0.97	(no data)		2.8	0.61–6.4
CPS (240:15 Hz, 12%)	0.18	0.09–0.28	(no data)		1.7	0.30–3.4
Taube (1992), rainbow trout (*Oncorhynchus mykiss*), 33 to 60 cm FL[g]						
100 to 121 μS/cm, 9 to 13°C						
DC	(no data)		(no data)		0.51	0.26–0.71
PDC (30 Hz, 50%)	(no data)		(no data)		1.4	0.90–4.8
PDC (30 Hz, 75%)	(no data)		(no data)		1.3	0.53–2.6
PDC (60 Hz, 50%)	(no data)		(no data)		0.73	0.54–1.3
CPS (240:15 Hz, 12%)	(no data)		(no data)		1.0	0.54–1.3
AC (60 Hz)	(no data)		(no data)		0.30	0.27–0.41
Meismer (1999), rainbow trout (*Oncorhynchus mykiss*), 21 to 50 cm TL[g]						
530 μS/cm, 18°C						
DC	0.05	0.03–0.07	0.17	0.12–0.21	0.53	0.34–0.63
PDC (15 Hz, 6%)	0.08	0.06–0.10	0.16	0.13–0.19	0.63	0.54–0.70
PDC (60 Hz, 24%)	0.04	0.03–0.05	0.07	0.05–0.09	0.16	0.14–0.20
CPS (240:15Hz, 12%)	0.10	0.06–0.12	0.21	0.18–0.26	0.56	0.43–0.69
Meismer (1999), Colorado pikeminnow (*Ptychocheilus lucius*), 30 to 39 cm TL[g]						
530 μS/cm, 18°C						
DC	0.09	0.05–0.13	0.16	0.14–0.19	0.38	0.28–0.57
PDC (15 Hz, 6%)	0.11	0.08–0.13	0.18	0.16–0.21	0.32	0.25–0.36
PDC (60 Hz, 24%)	0.05	0.02–0.10	0.16	0.09–0.20	0.22	0.18–0.27
CPS (240:15 Hz, 12%)	0.11	0.09–0.14	0.18	0.13–0.20	0.30	0.26–0.35
Ruppert and Muth (1997), humpback chub (*Gila cypha*), 5 to 10 cm TL[g]						
940 μS/cm, 15°C						
PDC (30 Hz, 12%)	(no data)		0.42	0.38–0.45	0.63	0.62–0.65
					(tet. 0.76	0.74–0.78)
PDC (60 Hz, 24%)	(no data)		0.36	0.35–0.38	0.56	0.53–0.62
					(tet. 0.75	0.71–0.82)
PDC (80 Hz, 40%)	(no data)		0.34	0.31–0.38	0.51	0.45–0.58
					(tet. 0.72	0.69–0.75)
CPS (240:15 Hz, 12%)	(no data)		0.47	0.43–0.53	0.67	0.65–0.69
					(tet. 0.80	0.76–0.83)

Table 2. Concluded.

Source, species, length conductivity, temperature Current[d]	Response threshold, peak V/cm[b] Twitch Mean	Range	Anodic taxis Mean	Range	Narcosis or stun[c] Mean	Range
Ruppert and Muth (1997), bonytail (*Gila elegans*), 5 to 8 cm TL[g]						
940 μS/cm, 15°C						
PDC (30 Hz, 12%)	(no data)		0.48	0.46–0.49	0.73	0.69–0.75
					(tet. 1.10	1.04–1.16)
PDC (60 Hz, 24%)	(not recorded)		0.45	0.43–0.46	0.61	0.60–0.64
					(tet. 1.00	0.95–1.04)
PDC (80 Hz, 40%)	(not recorded)		0.40	0.38–0.42	0.60	0.58–0.62
					(tet. 0.98	0.97–0.99)
CPS (240:15 Hz, 12%)	(not recorded)		0.78	0.75–0.80	1.00	0.98–1.04
					(tet. 1.40	1.38–1.42)

[a]Sternin et al. (1976, Appendix 4: data for many species, further summarized here for all species combined), Kolz and Reynolds (1989b, Figs. 6–10, data approximated from graphs), Taube (1992, Appendix Table 8), Ruppert and Muth (1997, Table 1), and Meismer (1999, Table 6; ranges by personal communication).
[b]Data from Sternin et al. (1976) may include mean PDC and AC (rms) voltage-gradient thresholds.
[c]Thresholds for narcosis and stun (narcosis and tetany combined) are assumed to be the same, but some data summarized for stun by Sternin et al. (1976) may represent the threshold for loss of equilibrium prior to narcosis. Distinct thresholds for tetany (tet.) from Ruppert and Muth (1997) are given in parentheses under narcosis thresholds.
[d]DC = direct current, PDC = pulsed direct current, CPS = Coffelt's complex pulse system (a PDC pulse train), and AC = alternating current. PDC parameters are pulse frequency and duty cycle.
[e]Data for only one species from only one investigation.
[f]Average of summarized data across species, not mean for individual specimens or treatments.
[g]Data from homogeneous-field experiments.
[h]Data from heterogeneous-field experiments.

160 μS/cm ranged from about 0.01 to 0.97 V/cm for twitch, 0.25 to 3.6 V/cm for taxis (DC and PDC only), and 0.08 to 10 V/cm for narcosis. In field and laboratory trials with a variety of species in water conductivities of 35 to 125 μS/cm, Fisher and Brown (1993) found that most fish were stunned with 60-Hz AC at minimum peak voltage gradients from 0.2 to 1.1 V/cm, the upper end of which matches Kolz and Reynolds' (1989b) range of stun threshold values for goldfish at 110 to 160 μS/cm (0.94–1.1 V_p/cm; Table 2). As water conductivities increase from very low levels, voltage-gradient-response thresholds decrease rapidly through 100 μS/cm, decrease more slowly through about 800 μS/cm or less, then stabilize at relatively low levels for all higher conductivities (Table 2).

Voltage-gradient thresholds reported for different (or even the same) types of currents are often difficult to compare among investigations due in part to differences in experimental conditions and methodology and the size, condition, and species of fish tested. With that in mind, data in Table 2 suggest that response thresholds are generally lowest for AC and often highest for DC (exceptions include DC thresholds occasionally as low as AC for twitch and lower than PDC for taxis). Thresholds for PDCs of various configurations vary widely from lowest (especially when compared only to DC) to highest, but in most comparisons, range between values for AC and DC. In comparisons among CPS, simple PDCs, and DC, taxis thresholds are almost always highest for CPS and usually lowest for simple (constant-frequency) PDCs, but narcosis thresholds vary from lowest to highest for CPS and simple PDCs and from intermediate levels to highest for DC. For goldfish, Kolz and Reynolds' (1989b) reported similar stun thresholds for AC and PDC within each range of conductivity from 110 to 10,000 μS/cm (Table 2). Jesien and Hocutt (1990) similarly found that 50%-tetany thresholds for catfish subjected to pulsed ACs (0.11 to 0.37 V_p/

cm) were nearly the same as those they determined for PDCs (0.09 to 0.28 V/cm). Interestingly, at comparable levels of conductivity, and regardless of current and waveform, Jesien and Hocutt's (1990) 50%-tetany thresholds for channel catfish are much lower than Kolz and Reynolds' (1989b) stun (narcosis) thresholds for goldfish (Table 2). However, the thresholds and effects of pulsed AC may be significantly different from those of continuous AC.

Vincent (1971) concluded that PDC induces DC-like responses but at lower field-intensity thresholds. As summarized in Table 2, this suggestion of lower thresholds for PDC than DC is supported by Kolz and Reynolds' (1989b) data for stun but not for twitch, for which PDC and DC thresholds are broadly comparable. Nor is Vincent's (1971) statement supported by the data of Sternin et al. (1976), which suggest lower thresholds for DC. For goldfish that were tested in approximately 300-μS/cm water with DC and a multitude of PDCs, Bird and Cowx (1993) reported threshold data (mistakenly attributed to crucian carp—Cowx, personal communication) that are very similar to those of Kolz and Reynolds (1989b), except Bird and Cowx observed a taxis response in PDC treatments and Kolz and Reynolds did not. Bird and Cowx (1993) found that DC and the various PDC threshold ranges were similar for twitch (0.04–0.08 V/cm) and taxis (0.10–0.20 V/cm) but not stun (DC threshold of 0.9V/cm was notably greater than the 0.2–0.6 V/cm thresholds for PDCs).

Within most species-size groups tested with DC, a wide variety of simple PDCs, and a PDC pulse train, Edwards and Higgins (1973) also found that stun thresholds (only response tested) were generally highest for DC and least for the PDC pulse train with mutually exclusive ranges (e.g., for 8–22-cm bluegill, stun thresholds were 1.3–1.9 V/cm for DC vs. 0.3–0.6 V/cm for the PDC pulse train). In a set of experiments with rainbow trout (31–48 cm FL) in premapped heterogeneous fields with DC, various PDCs, and CPS, Taube (1992) also found that the thresholds for stun and twitch (taxis not recorded) were generally highest for DC and lowest for a PDC pulse train, in this case CPS (Table 2). However, in a set of homogeneous-field experiments, also with rainbow trout (33–60 cm FL), Taube (1992) found the opposite, with stun thresholds notably lower for DC than CPS.

Relative to DC and a PDC pulse train, Edwards and Higgins (1973) found the ranges of stun thresholds among the various constant-frequency PDCs they tested for several species-size groups to be generally more variable. The threshold ranges were sometimes intermediate and sometimes matching or occasionally exceeding the ranges for either DC and the pulse train. However, among these PDCs, there was a tendency for the thresholds of lower-frequency currents to more closely approximate the higher threshold values for DC and the higher-frequency currents to approximate the lower threshold values for the PDC pulse train. Similarly, data in Table 2 suggest that response thresholds generally decrease with increasing pulse frequency. For example, Meismer (1999) consistently found twitch, taxis and narcosis thresholds for 60-Hz PDC notably lower than those for 15-Hz PDC, and the latter generally comparable to thresholds for DC and CPS (Table 2). Bird and Cowx (1993) observed the opposite tendency for twitch and taxis (thresholds increasing with increasing pulse frequency) among the PDCs they tested with a 10% duty cycle, but not PDCs with 50% or 90% duty cycle or for the stun thresholds.

In general, biologists have found that response thresholds vary with species and size of fish. Comparing twitch, taxis, narcosis, and tetany thresholds for two closely related endangered species of similar size (5–10 cm TL) but different ages, Ruppert (1996) and Ruppert and Muth (1997) reported that year-old humpback chub were 8 to 43% more sensitive to a variety of PDCs and CPS than 7-month-old bonytail. Differences were greatest for CPS and tetany treatments. With a few exceptions, Meismer (1999), who tested DC, 15 and 60-Hz PDC, and CPS, found that thresholds for Colorado pikeminnow (30–39 cm TL) were generally similar to thresholds for rainbow trout (21–50 cm TL) for twitch and taxis but not narcosis (narcosis thresholds were notably lower for Colorado pikeminnow). Edwards and Higgins (1973) also compared thresholds (stun only) among species but found that apparent differences were confounded by differences in the size of the fish that were tested. Combining data for currents and ignoring differences in species, they found that stun thresholds decreased with increasing fish length (e.g., 0.6 to 1.8 V/cm for 4 to 8-cm bluegill, 0.2 to 1.4 V/cm for 17 to 27-cm channel catfish, and 0.2 to 0.9 V/cm for 28 to 61-cm bowfin; water about 100 μS/cm, 24° C).

Consensus of biologists experienced in electrofishing and in general texts on electrofishing is that large fish are easier to capture than smaller fish. The relation is supported by at least some studies comparing the size distribution of fish collected by electrofishing with the known size distribution of populations or comparable data collected by other techniques (e.g., Sullivan, 1956; McFadden, 1961). Taylor et al. (1957) investigated the relation between DC response thresholds and fish length by subjecting 4 to 34-cm (probably SL) rainbow trout to homogeneous fields of 0.1 to 0.5 V/cm for up to 6 s. They recorded four levels of responses, from inhibited motion or minor signs of distress to narcosis or tetany, and reported decreasing response thresholds as size increased to 25 cm; beyond 25 cm the relationship was not clear. Similarly, Maxfield et al. (1971)

subjected young-of-the-year (YOY) rainbow trout averaging 5 cm TL to 30 s of homogeneous, 8-Hz PDC at 1 V_p/cm and yearlings averaging 19 cm TL to 5-Hz PDC at 0.75 V_p/cm, but despite the lower field intensity and slightly slower pulse frequency, they observed narcosis only among the yearlings. Lamarque (1990) noted that the threshold for nerve response deceases with increasing nerve length only for nerves shorter than about 4 cm and that the threshold remains constant for nerves of greater length. Accordingly, he concluded that any size-response relation (except for small fish) is probably due to factors other than the direct effect of the electric field on nerves. Emery (1984) suggested that the effect of size is a function of total surface area rather than the length or weight of the fish.

Zone of Reactive Detection

The outermost region of a heterogeneous electric field to which fish respond in some fashion is usually referred to as the zone of reactive detection, fright, or perception (Fig. 11). Field intensity in this zone is sufficient to elicit momentary involuntary twitches, shudders, or convulsions but low enough that fish can still remain mostly indifferent to the stimuli, move away voluntarily if irritated, or respond with instinctive reactions such as flight, taking cover, and possibly aggressive displays if startled. Fish might actually perceive the field but may or may not react to it at substantially lower field intensities and notably greater distances from the electrodes than is required to evoke twitches or fright responses. The commonly referenced threshold for the twitch response occurs when field intensity is sufficient to elicit a sudden movement, shudder, or muscular convulsion, the latter most likely occurs only when the current is switched on or off, pulsed, or possibly alternated with sufficient voltage differential. Although not indicated in Fig. 11, Sharber and Black (1999) consider at least some of the responses attributed to this zone, particularly twitch in the form of muscular jerks or convulsions, to be epileptic automatisms.

A fright response usually reflects the fish's normal behavior when startled. It is most likely an unconditioned defensive reaction (Sternin et al., 1972, 1976) that results in many fish escaping the more intense and effective portions of the field (Novotny and Priegel, 1974). Fright or other responses to detection of an electric field vary with species. Meismer (1999) observed that rainbow trout (21–50 cm TL) exposed to homogeneous fields of gradually increasing intensity in shallow test chambers (~2.0 x 0.5 x 0.5 m) reacted very violently with much thrashing, flailing, and rapid, forceful swimming, sometimes leaping 10 to 15 cm out of the water in an apparent attempt to escape the field. In a few cases, swimming was so forceful that the fish broke through nylon-mesh screens intended to prevent fish from contacting the electrodes. In contrast, similarly treated Colorado pikeminnow (30–39 cm TL) reacted much less violently without thrashing, jumping, trying to break through screens, or otherwise desperately trying to escape. Vibert (1963) noted that flatfishes may take cover by burrowing. In some cases, the fright response attributed to an electric field might actually be a reaction to noise, motion, or related, nonelectrical stimuli produced during an electrofishing operation.

Some biologists (e.g., Reynolds, personal communication) suspect that fish in this zone cannot perceive a directional component to the electric field. If so, fish may be just as likely to dart farther into the field as away from it. However, if fright response or flight results in escape by most fish in this zone, then the majority of fish captured by electrofishing were probably present in the effective zones of the field (taxis, narcosis, and tetany) when the current was switched on. Captured fish initially in the zone of reactive detection may have been trapped against a shoreline, bar, shallow riffle, or purposely set net as the electric field approached. Such possibilities should be considered when planning the approach to a sampling area and deciding where, when, how often, and how long the electric field should be applied.

Zones of Undirected or Inhibited Swimming and Taxis

The combined zones of undirected motion or inhibited swimming and taxis (forced swimming towards the anode, anodic taxis, electrotaxis, or oscillotaxis) represent the epileptic phase of automatism according to the Bozeman paradigm (Sharber, personal communication; Sharber and Black, 1999). Without introducing a nonelectrical stimulus, it might be difficult to behaviorally distinguish fish that respond indifferently to an electric field in the zone of reactive detection from those that exhibit undirected or inhibited motion in the portion of the zone of automatism represented by undirected or inhibited swimming. Fish in the latter state may blunder (Northrop, 1967) into the zone of taxis or be engulfed by that portion of a moving field and subsequently be forced to swim towards the anode until they are netted or reach the zone of narcosis. Some fish exhibiting taxis have enough momentum to carry them through the zone of narcosis into the zone of tetany. The threshold for taxis by targeted fish defines the outer limits of an effective electrofishing field.

Vibert (1963) noted that flatfishes "may burrow or remain on the bottom resisting the swimming response until narcosis or tetany take over." Whether flatfish actually resist taxis, respond in a different, perhaps species-

specific manner, or experience different electrical-field parameters at the substrate interface is unknown.

Haskell et al. (1954) suggested that due to continually changing orientation of a fish's body, especially in a moving field, taxis towards the anode in DC and PDC is a composite of natural swimming movements caused by the central nervous system, involuntary bends of the body toward the anode (especially upon initial circuit closure in DC and with each pulse in PDC), and anesthesia (narcosis). They reported that involuntary bends toward the anode were strongest when fish were perpendicular to the lines of current, whereas the anesthetic response was greatest when fish were parallel to the lines of current.

Lamarque (1990) suggested that anodic taxis under PDC is distinctly different from that under DC. Haskell et al. (1954) also observed differences and concluded that DC "modifies the normal swimming motion and guides the fish toward positive pole," whereas PDC causes an "involuntary . . . turn toward the positive pole and forward motion at each circuit closure." Haskell et al. (1954) and Lamarque (1990) also noted that motion resulting from PDC required a lower voltage threshold and was more pronounced than that from DC. Some biologists (e.g., Fredenberg, personal communication) have observed that taxis can be so powerful in some PDC currents that fish sometimes appeared to swim rapidly by and beyond the anode without succumbing to narcosis or tetany (sometimes ultimately circling back towards the anode). Other biologists reported no taxis under PDCs for certain species and experimental conditions (e.g., Kolz and Reynolds, 1989b, 1990a for goldfish). In AC, taxis cannot be sustained towards either electrode because the current continually reverses direction and the fish ultimately aligns itself perpendicular to the lines of current in a "swimming" response referred to as transverse oscillotaxis.

Zones of Narcosis and Tetany

Narcosis and tetany represent two distinct forms of stunned immobility (Vibert, 1963). The zone of narcosis or petit mal (Sharber, personal communication; Sharber and Black, 1999) is characterized by a loss of equilibrium, limp or relaxed muscles, and reduced or discontinued breathing motions (apnea). The zone of tetany or grand mal (Sharber, personal communication) is represented by a partial to full state of sustained muscle contraction. In full tetany, fish are rigid and apnea persists. Fish in the outermost, (lowest intensity) portions of the zone of tetany sometimes quiver or exhibit a very confined and rapid swimming motion, usually while lying on their sides or backs. Although treated here as the initial phase of tetany or grand mal, Biarritz researchers considered it a separate transitory response between narcosis and tetany and referred to it as pseudo-forced or second swimming towards the anode. Similarly, Sharber and Black (1999), in accord with conventional epilepsy terminology, considered it as a transitory phase of tonic-clonic contractions between petit mal and grand mal. During this transitory phase or as fish progress from it to a state of full tetany or grand mal, Sharber and Black (1999) also noted that chromatophore stimulation can result in a patchy or barlike discoloration of the skin (brands).

When fish in narcosis or the beginning of tetany are removed from the electrofishing field (by netting, switching off the current, or moving the field away from the fish), they usually recover immediately and behave in a relatively normal manner. For goldfish ($\bar{x}$ = 16 cm) exposed for 5 s at 1.1 V_p/cm (294–320 μS/cm; 16–18° C), Bird and Cowx (1993) reported that recovery of breathing motions was immediate after exposure to DC but variously delayed from 4 to 45 s after exposure to various PDCs. Mitton and McDonald (1994a) similarly reported ventilation recovery times averaging 19 s (but sometimes requiring up to 3 min) for rainbow trout exposed to 20 s of 60-Hz PDC at a field intensity sufficient to induce tetany. Barham et al. (1989b) reported that over a wide range of field intensities and exposure times in 50-Hz AC and 50-Hz, half-sine PDC, common carp (25–60 cm) shuddered convulsively a few seconds after current ceased and recovered respiratory motions within 30 to 100 s but otherwise remained narcotized for an additional 2 to 40 s; recovery of equilibrium and swimming motions took another 4 to 44 s. Meismer (1999) noted that adult rainbow trout recovered equilibrium immediately after being narcotized at threshold level for 5 s in DC or CPS, but that recovery was somewhat delayed in 15 or 60-Hz PDC.

Fully tetanized fish or those in the zone of tetany for excessive periods may require several minutes to recover normal muscle response, respiratory movements, and equilibrium. Full physiological recovery takes much longer, more than 24 h according to Barton and Dwyer (1997). Some fish kept in a state of tetany too long never recover. Meismer (1999) reported that among Colorado pikeminnow (30–39 cm TL) and rainbow trout (29–50 cm TL) subjected to gradually increasing field intensity through the threshold for tetany, then held at 1.0 V_p/cm for 5 s in DC, 15- or 60-Hz, square-wave PDC, or CPS, all Colorado pikeminnow exposed to 15-Hz PDC or CPS required more than 5 min to recover equilibrium, some individuals of both species exposed to 60-Hz PDC required more than 15 min to recover equilibrium, and 10% of rainbow trout exposed to the 60-Hz, square-wave PDC died. Among specimens of each species tetanized with abrupt 10-s exposures of 60-Hz, square-wave PDC (via Coffelt's VVP-15) or 60-Hz, quarter-sine-wave PDC (via Smith-Root's GPP 5.0) at 1.5 V_p/cm, Meismer (1999)

reported that all fish recovered equilibrium except 30% of the rainbow trout exposed to 60-Hz, square-wave PDC.

Like electrofishing, fishery biologists have found immobilization by controlled electrical narcosis to be a useful tool when tagging fish, gathering specimen-specific data, or collecting eggs and milt from fish, especially large fish (Hartley, 1967; Gunstrom and Bethers, 1985; Barham et al., 1987, 1988, 1989a; Orsi and Short, 1987; Walker et al., 1994). The technique is usually referred to as electrical anesthesia, but Hartley (1967) emphasized that although the fish are temporarily paralyzed and appear unconscious, we do not know whether they are insensitive to touch or pain. For anesthesia, fish are usually subjected to a relatively homogeneous electric field in a small chamber where voltage gradients are easily controlled. Generally, smooth DC is preferred to minimize the risk of tetany and because the operator can handle the fish in the water without feeling the current, unless he has cuts on his hands (Hartley, 1967). According to Hartley (1967) and Kynard and Lonsdale (1975), fish can be instantly immobilized by initially applying twice the minimum voltage subsequently needed to maintain narcosis. These voltage levels are arrived at experimentally or through experience and depend primarily on water conductivity, species, and size of the fish. Unless fish are physically restrained, the higher initial field intensity is probably necessary because many fish will not be aligned parallel to the lines of current when the field is switched on. Ellis (1974) narcotized 2-year-old channel catfish with 60 s of 60-Hz AC, 15 to 25-Hz PDC, or DC at 1.5 V/cm then monitored the fish in cages in a pond for 133 days. He reported that the fish regained consciousness within 2 h and exhibited no significant effects on survival, growth, and feed conversion. Barham et al. (1987, 1988, 1989a,b) found anesthesia in both AC and half-sine PDC preferable to benzocaine for Mozambique tilapia, but unsuitable for common carp. Tipping and Gilhuly (1996) noted that in preliminary experiments with adult steelhead (rainbow trout), electrical anesthesia using CPS at a calculated 1.7 V_p/cm produced better narcosis than carbon dioxide anesthetization but also induced compression fractures in the spines of 8% of the fish.

Lamarque (1967a, 1990) observed that in a DC field just sufficient for narcosis, a fish facing the anode can remain safely narcotized for several hours. However, Kynard and Lonsdale (1975) reported that yearling rainbow trout (~12 cm) held under DC narcosis for 6 h (0.25 V/cm, 13–21° C, 450 µS/cm) suffered 7% mortality and that survivors required up to half a day to resume normal swimming and feeding behavior, but that growth and phototropic response over the next 25 days were unaffected. In contrast, recovery was generally instantaneous for fish narcotized for only 1 or 2 h and no mortalities were reported for trout held under electrical narcosis for up to 4 h. Kynard and Lonsdale (1975) also documented a decrease in ventilation rate for narcotized fish, up to 52% reduction for yearlings held under narcosis for 4 h versus an 18% decrease among controls.

Walker et al. (1994) investigated the use of homogeneous 50-Hz ACs (sine and triangular waveforms) and 50-Hz PDC over a range of field-intensities and exposure times for successful narcosis (anesthetization) of northern pike juveniles and adult broodstock. Their criterion for successful narcosis was sustained immobilization for at least a minute after exposure without externally obvious physical injury (enough time to strip adults of eggs or milt). Fish were oriented parallel to lines of current and faced the cathode in PDC. For juveniles (13–19 cm SL), the field intensities and exposure times that induced narcosis or injury using either AC were variable and unpredictable (e.g., injury after 30-s exposure at 0.4 V_{rms}/cm, narcosis without injury after 60 s at 0.7 V_{rms}/cm, and neither narcosis nor injury after 30 s at 2.1 V_{rms}/cm). In contrast, 10- to 60-s exposures of juveniles to the PDC over a range of 0.4 to 2.1 V_p/cm produced no externally detected injuries or obvious behavioral impairments and at 1.4 V_p/cm or greater, consistently induced successful narcosis. Post-exposure narcosis time increased with increasing field intensity from just under 2 min after a 10-s exposure at 1.4 V/cm to 12 min after a 60-s exposure at 2.1 V/cm. Although 10-s exposures always resulted in the shortest times, narcosis time was not statistically correlated with time of exposure. Walker et al. (1994) also exposed over 300 broodstock northern pike (45–97 cm SL) to 10-s exposures of the PDC and successfully narcotized them for approximately a minute with breathing movements reestablished within 2 min and upright swimming within 3 min. There were no deaths or external signs of injury within 24 h of exposure, but the fish were not X-rayed to assess internal injuries.

Another method to anesthetize fish is to place them in direct contact with the electrodes, usually on a table with the anode contacting the head and the cathode contacting the body (Kolz, 1989b). As long as the body of the fish conducts an adequate current, the fish is immobilized; when the circuit is broken, the fish recovers instantly unless it was maintained under narcosis more than a couple of hours.

The terms narcosis and tetany are often confused and used interchangeably in practice and in the literature. In some cases, failure to distinguish these terms is due to difficulty in identifying the initial states of partial tetany. The terms stun or stunned are used herein to refer to immobilization (paralysis) in either state when the distinction is unnecessary or the specific state is undefined. The term shock is sometimes used as a synonym for stun (Sternin et al., 1976), but it is more generally defined as any response to an electrical stimulus

(especially a sudden reaction), the electrical stimulus producing such a response, and, among fish biologists, as the act of electrofishing.

Comparison of Currents for Electrofishing Purposes

AC is often considered to have a larger effective field than either DC or PDC (Lamarque, 1990), but at the same mean output (voltage, amps, or watts) this might not always be the case relative to DC and is unlikely relative to most PDCs. Kolz and Reynolds (1989b) found peak-voltage gradient thresholds for narcosis in goldfish were lower in AC than in DC but except at the lowest conductivities, comparable to those in PDC (Table 2; Figs. 14 and 15). Also, as discussed earlier, the effective anodic fields for DC and PDC include the zone of taxis whereas the effective fields around electrodes for AC are limited to narcosis and tetany. Kolz and Reynolds (1989b, 1990a) found that the DC threshold for taxis in goldfish (0.7 V_p/cm) is lower than the threshold for AC narcosis (0.9 V_p/cm), hence a slightly larger effective field for DC if peak outputs are the same. Ignoring taxis and assuming equal peak-field-intensity thresholds for narcosis, the same peak output, and all other conditions the same, distribution of peak-field intensity (voltage gradient, current density, or power density) and the size of the effective field will be identical regardless of the type of current and waveform. However, if mean (rms for AC) rather than peak output are matched (generator capacity is limited mostly by mean output), distribution of peak-field intensity and size of the effective field will always be greater for AC and PDC than for DC (peak and mean output or field intensity are identical for DC, and, in this case, distribution of mean-field intensities would be the same for all currents). For AC and PDC, the difference between peak and mean output and field intensities varies according to waveform characteristics and is frequently greater, sometimes much greater, for PDC. For single-phase sinusoidal AC, peak-voltage gradient and peak-power density are about 1.4 and 2 times greater, respectively, than corresponding mean values (for sinusoidal AC, $V_{rms} = 0.71\ V_p$) or square-wave PDC with a 71% duty cycle. Likewise for peak-voltage and peak-power output. If a PDC duty cycle is less than 71% (regardless of wave shape), its peak-field intensity will always be greater than in sinusoidal AC fields at the same mean output. For example, with a 25% duty cycle, square-wave PDC fields will have a peak-voltage gradient and peak-power density about 2.8 and 8 times greater, respectively, than sinusoidal AC and 4 and 16 times greater, respectively, than for DC or corresponding mean values for this PDC.

In some cases, larger fields might not be advantageous. Vincent (1971) suggested that because the zones of narcosis and tetany, as well as taxis, are larger in PDC than DC fields, fish might be more difficult to net and more susceptible to tetany and tissue damage. Stunned fish are usually easier to net than rapidly moving fish in taxis, but fish that are stunned beyond the reach of netters may not be seen and escape capture. Chmielewski et al. (1973) noted that fish stunned while taking cover are less likely to be captured, and those initially stunned in flowing water may be washed away before they can be netted.

Although Haskell (1950) suggested that DC is more dangerous to man than AC, most electrofishing authorities consider AC, with its reversing polarity and presumably large zone of tetany, to be more dangerous to fish and perhaps to the electrofishing team and observers than either DC or PDC (e.g., Hauck, 1949; Taylor et al., 1957; Lamarque, 1967a, 1990; Northrop, 1967; Vibert, 1967b; Vincent, 1971; Novotny and Priegel, 1974; Reynolds, 1983, 1996; Kolz et al., 1998). Lamarque (1967a) specifically observed that AC and PDC can provoke violent tetanus. As discussed later, excessive exposure to tetanizing currents can result in severe stress, unrecoverable fatigue, or respiratory failure. Still, some state agencies (e.g., Illinois, Michigan) continue to make extensive use of AC electrofishing (Schneider, 1992). Hudy (1985) and Schneider (1992) maintain that AC can be used effectively without significant harm to the populations being studied. If so, the substantial zones of narcosis and tetany in AC might be desirable to improve capture efficiency under certain conditions–usually in shallow, clear, slow-moving water where fish can be easily netted and rapidly removed from the electric field. In low-conductivity streams along the Appalachian Mountains, where AC is considered the most effective electrofishing current, experienced field biologists report few, if any, mortalities, brands, or other external signs of injury because they are able to net the fish quickly and minimize time of exposure (Wydoski, personal communication). However, as discussed later, spinal injuries, which may not be externally obvious, are not necessarily dependent on time of exposure and if AC's reputation for causing greater harm than DC or PDC is warranted, its use is probably best reserved for situations in which fish will be permanently removed and injuries or mortalities are not a serious concern (McCrimmom and Berst, 1963).

In most electrofishing operations, taxis and narcosis are the responses to be sought and optimized, whereas tetany is considered dangerous and to be minimized or avoided. DC is generally considered the least damaging current, in part because it is believed to have a higher threshold for tetany than AC or PDC. Grisak (1996), who

noted that all fish he captured with PDC or DC succumbed to tetany, observed that in PDC (40-Hz), most fish reacted mildly and appeared to simply rise from the depths to the surface (apparently tetanized on the spot some distance from the anode), except common carp which at the surface swam violently away from the electric field (no carp were captured). In contrast, he observed that most fish in DC swam directly toward the anode and some, particularly goldeye, swam so strongly that once stunned near the anode, momentum frequently carried them into contact with the anode. As discussed earlier, the zone of tetany for any current can be controlled to some degree by careful selection of output voltage and the size, shape, and configuration of the electrodes (Novotny and Priegel, 1971, 1974; Chmielewski et al., 1973; Novotny, 1990). Lamarque (1990) suggested that DC generated by full-wave rectification of three-phase AC (600 Hz) has less ripple (4%) and a correspondingly less tetanizing effect on fish than DC that is only half-wave rectified (300 Hz, 17% ripple).

PDC is a diverse family of waveforms with different wave shapes, simple and complex frequencies, pulse widths, and duty cycles, each of which might affect the responses of fish in the electric field. In sea water (>50,000 µS/cm), Groody et al. (1950) compared the responses of Pacific sardine (20–30 cm) and topsmelt (11–12 cm) in DC and several PDC and hybrid currents (3–12-Hz, square-wave PDC with various pulse widths, some hybridized with lower-intensity DC; 45–68-Hz, half-sine-wave PDC—half-rectified AC; 120-Hz, half-sine-wave PDC—fully rectified AC; the latter as a pulse train switched on and off at 3–30 Hz; and 4–8-Hz, exponential PDC). They reported that square-wave PDCs were by far best at inducing taxis (observed in 36% of the fish vs. none to 3% for the other currents, including 3% for DC). Most effective and least injurious of all currents tested were 3- to 4-Hz, square-wave PDCs with 67 to 75% duty cycles (168–250-ms pulses). Groody et al. (1950) also observed that the strength of current most effective in producing taxis was inversely related to the size of the fish. In fresh water, Haskell et al. (1954) tested brown trout (8–18 cm) in fields of square-wave PDC at frequencies of 60 Hz or less but observed no significant reactions until the frequency was reduced to about 15 Hz, after which response strength increased as the frequency was further reduced to 1 or 2 Hz with an 80% duty cycle (800 and 400 ms for latter frequencies). Perhaps as pulse duration increases in high-duty-cycle currents, fish respond more as normally expected with DC in fresh water. Kolz and Reynolds (1989b) also failed to observe taxis among goldfish (6–9 cm TL) subjected to 50-Hz, square-wave PDC (duty cycles of 10, 25, and 50% and pulse widths of 2, 5, and 10 ms, respectively), but they did document twitch responses and narcosis; all three responses were observed in DC.

Contrary to the preceding findings, other researchers have reported not only twitch or random movement, narcosis, and tetany but substantial taxis for PDC frequencies over 20 Hz. Vincent (1971) concluded that with frequencies at or below 50 Hz, PDC is as effective or more effective than DC in producing anodic taxis. Based on experiments with trout (brown or rainbow, 20 cm) at 18° C, Lamarque (1976) concluded that the optimum PDC frequency for taxis was around 100 Hz (30% duty cycle, 3-ms pulses), but he noted that lower frequencies might be better for electrofishing because tetany would be less likely near the electrode (higher threshold for tetany at lower frequencies). In contrast, Northrop (1962, 1967) found that square-wave PDC was most effective at inducing taxis in brown trout (20–25 cm) when operated at 33 Hz with a 67% duty cycle (20-ms pulse width) and that fish were immediately stunned and showed no significant electrotaxic behavior when subjected to 100-Hz PDC with a 50% duty cycle (5-ms pulse width). Perhaps when using 100-Hz PDC, Northrop's effective zones for both taxis and narcosis were so large, so distant from the anode, that he only observed and netted narcotized fish; that is, taxis may have occurred beyond his range for observing and netting fish. Based on field observations, Sharber (personal communication) found that taxis in square-wave PDC is not only evident at 60 and 30 Hz, but also much better than at 15 Hz (duty cycles of 24, 12, and 6%, respectively; pulse width 4 ms each). Based on mean times for rainbow trout to swim toward the anode and succumb to narcosis in raceway experiments, Sharber et al. (1994) reported that 30-Hz and 60-Hz PDCs (as well as CPS) were equally effective for taxis in rainbow trout (25–35 cm). Bird and Cowx (1993), unlike Kolz and Reynolds (1989b), documented taxis, as well as narcosis, in goldfish ($\bar{x}$ = 16 cm) under a variety of PDC waveforms and frequencies (30–600-Hz square, 50-Hz quarter-sine, 50-Hz exponential; pulse widths 0.2–30 ms). Ruppert (1996) and Ruppert and Muth (1997) also observed taxis in juvenile 5- to 10-cm humpback chub and bonytail subjected to 30-, 60-, and 80-Hz PDC, as well as CPS (4-, 4-, 5-, and 2.6-ms pulses, respectively). Similarly, Meismer (1999) documented taxis in adult rainbow trout and large subadult Colorado pikeminnow subjected to 60-Hz, square-wave PDC, as well as 15-Hz PDC and CPS.

Taylor et al. (1957), using a triangular PDC waveform and a fixed duty cycle of 33%, not only observed taxis in rainbow trout (20 cm) at frequencies as high as 120 Hz, but also reported lower thresholds for strong taxis at 48 to 120 Hz (0.33–0.25 V_p/cm) than at 36, 24, and 12 Hz (0.48, 0.78, and 0.87 V_p/cm, respectively). A similar inverse relation between frequency and voltage-gradient

thresholds was observed for narcosis. Although differences were sometimes not very great (and probably not significant), tendencies for similar inverse relations were reported by Taube (1992) for narcosis (no data for taxis) in adult rainbow trout subjected to homogeneous fields of 30- and 60-Hz PDC, Ruppert and Muth (1997) for taxis and narcosis in juvenile bonytail and humpback chub subjected to 30-, 60-, and 80-Hz PDC, and Meismer (1999) for twitch, taxis, and narcosis in adult rainbow trout and in large subadult Colorado pikeminnow subjected to 15- and 60-Hz PDC. Taylor et al. (1957) also reported that for currents of the same pulse frequency, those with greater duty cycles (47 and 88%, resulting from greater pulse widths) also had higher thresholds for taxis and were therefore less efficient at inducing taxis (smaller effective ranges from anode). This relation between duty cycle (or pulse width) and taxis thresholds for currents of the same pulse frequencies has not been reported by other investigators. However, data by Kolz and Reynolds (1989b), who assessed response thresholds for goldfish subjected to 50-Hz PDC with duty cycles of 10%, 25%, and 50% and failed to observe taxis, suggest no similarly consistent relation for either twitch or stun thresholds.

As might be expected based on the above discussed relation between threshold levels and PDC frequency, some researchers have found PDCs less than 20 Hz to be less effective for taxis and capture of fish than higher-frequency PDCs. Northrop (1967) reported poor taxis for frequencies of 10 Hz or less and Sharber (personal communication) suggested that taxis using 15-Hz PDC is unsatisfactory for effective electrofishing.

Like low-frequency PDCs, CPS, with its train of three 240-Hz pulses delivered 15 times per second, has also established a reputation for poorer performance than higher-frequency PDCs. In one-on-one boat-electrofishing comparisons in Alaskan streams, Taube (1992) reported catch rates 56 to 68% lower for CPS than DC or 25-Hz PDC, but he failed to report whether peak outputs or field strengths were the same. Ruppert and Muth (1997) reported higher thresholds for taxis in juvenile humpback chub and bonytail subjected to CPS than 30-, 60-, or 80-Hz PDCs. Similarly, Meismer (1999) found twitch, taxis, and narcosis thresholds for adult rainbow trout and subadult Colorado pikeminnow generally much higher under CPS than 60-Hz PDC but comparable to those under 15-Hz PDC and DC. Perhaps the pulse trains of CPS are physiologically similar to single pulses in low-frequency PDC; if so, fish might be expected to respond to CPS as if the current were a simple 15-Hz PDC. However, despite reporting taxis thresholds similar to those for 15-Hz PDC, Meismer (1999) noted that once established, taxis under CPS did not appear to be quite as strong as under either 15 and 60-Hz PDC.

As noted above and contrary to Meismer's (1999) observation, Sharber et al. (1994) conducted raceway time trials with rainbow trout and concluded that taxis is comparable under 30-Hz PDC, 60-Hz PDC, and CPS, but they failed to note that field intensity under CPS had to be about 20% greater to initiate that taxis (Sharber, personal communication). Consistent with this observation, Meyer and Miller (unpublished manuscript, 1991; also Wyoming Game and Fish Department, 1991) used output voltages about 20 to 25% higher for CPS (460–470 V) than 40-Hz PDC (370–390 V) to maintain comparable sampling efficiency. In a set of heterogeneous-field experiments, Taube (1992) doubled output voltage for CPS to elicit electrofishing responses comparable to those for DC and 20- to 60-Hz PDC. Whether increasing field intensity would similarly improve taxis and capture efficiency under simple low-frequency PDCs (e.g., 15 Hz) has not been documented.

Electrofishing efficiency apparently varies with species, habitat, and timing as well as the electric field. Although Pugh and Schramm (1998), like other investigators discussed above, found 15-Hz PDC often less effective for capture of some species (especially shad, Clupeidae) and generally took fewer specimens overall than 60-Hz PDC in the lower Mississippi River, they reported that 15-Hz PDC actually captured a slightly greater diversity of species (35 species vs. 33 species for 60-Hz), was nearly as effective for many species, and was usually more effective for flathead catfish and blue catfish than 60-Hz PDC. Vincent (1971) concluded that DC is the best current for capture efficiency in rivers with brushy bank cover or high turbidity, whereas PDC is best in large open rivers with less bank cover and clearer water or in waters that are too conductive for effective use of DC. He also observed that a hybrid DC-PDC current (e.g., Fig. 5J) has qualities intermediate to DC and PDC, implying that it might be a good compromise. Roach (1992) and Reynolds et al. (1992) reported capture of three times more northern pike with 60-Hz PDC (50% duty cycle; 3 fish/h) than with either DC (0.9 fish/h) or 30-Hz PDC (25% and 75% duty cycle; 1.1 and 0.9 fish/h, respectively). Roach (1992) also noted that there is a general belief that 60-Hz PDC has better holding power than 30-Hz PDC and that when electrofishing conditions for capture of northern pike are ideal (timing), capture rates can be as high as 30 per hour using 60-Hz PDC (Roach, personal communication).

Results — Harmful Effects of Electrofishing on Fish

Possible detrimental effects of electrofishing on individual fish include cardiac or respiratory failure, injury,

stress, and fatigue. Mortality can be immediate or delayed. Small fish whose normal behavioral responses are slowed or inhibited may be more susceptible to predation. Fish that survive despite electrofishing injury or other adverse impacts, may suffer short-term, long-term, or lifetime handicaps that affect their behavior, health, growth, or reproduction. Significant numbers of surviving but adversely affected fish may ultimately impact community structure, population size, quality of the fishery resource, and management strategies. Harmful effects on fish (except embryos) reported in published literature, agency reports, and personal communications are summarized by species in Appendix B. For most pertinent investigations discussed in the remainder of this review, Appendix B also includes (if provided by the source) selected specimen, environmental, and electrical data that might not be referenced in the text.

In most cases, the harmful effects of electrofishing can be traced to one of two causes–excessive exposure to high intensity portions of electric fields resulting in tetany or aspects of electric fields that result in sudden and powerful, but unsustained, contractions of the body musculature, sometimes referred to as myoclonic jerks or seizures. The field characteristics and specific mechanisms responsible for the muscular convulsions have not been conclusively identified, but field intensities for these responses apparently extend well below those for tetany, perhaps even beyond the threshold for taxis in DC and PDC. Injuries due to such seizures are generally classified as spinal injuries but may include damage to tissues or organs not associated with the vertebral column (or notochord in cartilaginous fishes).

Effects Other Than Spinal and Related Injuries

Among nonspinal injuries, the most extreme would probably be electrocution when fish are sufficiently exposed to very high voltage gradients. In humans and other mammals, fibrillation of the heart and death by cardiac arrest are common results of exposure to strong electric currents, but electrofishing mortalities are generally rare, and such effects in fish are inadequately documented in the published literature. Northrop (1962, 1967) suggested that "temporary" cardiac arrest might occur in electrically narcotized (perhaps tetanized) fish, whereas Kolz and Reynolds (1990b) stated that cardiac arrest is seldom a factor in fish mortality. However, neither evidence nor references were provided to support either statement.

Based on an experiment with tetanizing DC on a rainbow trout, Taylor et al. (1957) reported that although they observed an arrhythmia (an extra beat followed by skipped beats) when the current was initially applied, normal heart beats quickly resumed as the current continued to be applied. They concluded, based on this one experiment, that the heart was not severely affected by electrofishing currents. However, the kymogram in their paper indicates that the current was interrupted momentarily after its initial application, skipped heart beats continued during that interruption, and normal beats resumed only after the current was reestablished. The events in Taylor et al.'s (1957) experiment are open to alternative interpretations, none of which can be effectively supported by a single kymogram. Perhaps cardiac arrest had indeed occurred, and the next impulse was required to start the heart again. In any case, the effects of an electric field on a fish's heart might be different using PDC or AC.

In experiments by Schreck et al. (1976) recovery of normal heart activity required much more time. Their fish also exhibited irregular cardiac activity immediately after being shocked (probably tetanized) with DC but required 4 to 5 min to return to normal. For two fish that were shocked for 45 and 60 s and failed to resume respiration, heart beats initially appeared to recover, then decreased in frequency and amplitude, and finally ceased in about 15 to 25 min (probably due to lack of oxygen).

The visceral organs of fish may also be affected by electric fields. Shparkovskij and Vataev (1985) stimulated the brain of Atlantic cod using square-wave PDC of 0.1 to 0.5 mA and a "burst" frequency of 300 Hz (in this case, the meaning of "burst" is uncertain). When lateral areas of hindbrain and midbrain were stimulated, peristalsis of the stomach and gut was inhibited. When the rostral cerebellum was stimulated, muscle contraction of the digestive tract was accelerated. Marriott (1973) described two ripe female pink salmon that had been electrocuted with 110-V, 60-Hz AC as having severely ruptured internal organs. However, Taylor et al. (1957) compared sections of various organs and tissues from an electrocuted rainbow trout with those from an untreated trout and reported no abnormalities.

Bleeding from the gills was perhaps first reported as an electrofishing injury by Hauck (1949) in his description of injuries to rainbow trout. Barham et al. (1989b) reported bleeding from the gills of many common carp narcotized with either 50-Hz AC or 50-Hz, half-sine PDC. However, this injury seems to be particularly prevalent in mountain whitefish electrofished in Montana regardless of the type of current or equipment used (Fredenberg, personal communication). According to Fredenberg (personal communication), "it is not unusual, on some streams, to see literally dozens of mountain whitefish come to the electrode under taxis with blood streaming in the water." The injury apparently occurs at field intensities much less than required for narcosis. However, neither the

specific cause of this injury nor its relation to other types of electrofishing injuries or subsequent survival has been investigated.

Walker et al. (1994) reported hemorrhages in both paired and median fins of juvenile northern pike exposed to 50-Hz, triangular-wave AC but not 50-Hz, sine-wave AC or 50-Hz PDC. Such injuries are likely often overlooked and may be more common than reported in the literature.

Respiratory failure is probably the ultimate cause of mortality in most electrically stunned fish. Because respiration may be reduced in partially narcotized fish and effectively ceases in fully narcotized or tetanized fish, those that are stunned but not removed from the electric field soon enough will likely die of asphyxiation. Synaptic fatigue occurs when fish are overexposed to a tetanizing current and results in a continuation of tetany for an extended period after removal from the field, a condition referred to as post-tetanic potentiation (Lamarque, 1990). Schreck et al. (1976) observed that after the current was switched off, tetanized rainbow trout either did not resume breathing movements for 60 s or they "coughed" violently for the first 30 s. Once respiratory movements resumed, hypoxic conditions were addressed by substantially increased buccal pressure rather than breathing frequency. However, other biologists reported increases in respiratory rates during recovery (e.g., Kraiukhin and Smirnova, 1966; Kynard and Lonsdale, 1975). Kolz and Reynolds (1990b) noted that oxygen debt can take hours to pay back. Respiratory failure in eels, and perhaps certain other fishes, can also be caused by a suffocating excess of mucus produced on the gills while under the influence of an electric field (Lamarque, 1990).

Stunned fish should be removed quickly from the electric field and placed in an uncrowded tank or pen with fresh, well-oxygenated water for recovery. Chmielewski et al. (1973) noted that trout not breathing (through the gills) for 5 min have little chance of survival without artificial respiration (e.g., moving fish back and forth or otherwise pumping or forcing fresh, oxygenated water over the gills). Based on experiments with brown trout, they reported that reestablishment of equilibrium and normal respiratory movements usually required under 1 to 2 min and that recovery time increased with field intensity and fish length but decreased with successive exposures (indicating decreased sensitivity to the electric field). For rainbow trout ($\bar{x}$ = 126 g) exposed for 20 s to 60-Hz PDC at a field intensity sufficient to induce tetany within 2 to 3 min, Mitton and McDonald (1994a) reported ventilation recovery times averaging 19 s but sometimes up to 3 min after removal from the current. Northrop (1967), however, noted that recovery from AC-induced electronarcosis (probably tetany) is relatively slow, taking as long as 5 to 10 min for some larger species. Schreck et al. (1976) noted a similar "apparent" recovery time for yearling hatchery-reared rainbow trout subjected to DC. Adams et al. (1972) narcotized 5- to 9-cm-TL common shiners, with 5- to 30-s exposures in homogenous fields of DC at about 1.5 to 3.6 V/cm and found that recovery times increased with field intensity, exposure time, and length of the fish. Shiners requiring over 2 min for recovery frequently died. In a set of homogeneous-field experiments, Bird and Cowx (1993) exposed goldfish ($\bar{x}$ = 16 cm) to 5 s of DC and various frequency, duty cycle, and types of PDC at a fixed field intensity of 1.1 V_p/cm. They reported that recovery of breathing motions (recovery of equilibrium not noted) was immediate for DC, and variously delayed 4 to 45 s for the various PDCs tested. Among the latter, respiratory-movement recovery times were greatest for 50-Hz, 25%-duty-cycle (5-ms pulses), quarter-sine PDC and shortest for the highest-frequency (400- and 600-Hz), highest-duty-cycle (90%, 2.3- and 1.5-ms), square-wave PDCs (6 and 4 s), and intermediate for all other PDCs tested (13 square-wave and one exponential, Appendix B). For square-wave PDCs with frequencies of 100, 400, and 600 Hz, breathing-movement recovery times decreased with increasing pulse frequency when duty cycle was 10% or 90% but remained the same as for lower frequencies when duty cycle was 50%.

Stress and fatigue are physiological responses that disrupt physicochemical balance, osmoregulatory functions, and normal behavior but usually require only a short time for recovery. According to Vibert (1967b), Halsband reported that the average duration of residual effects after fish were stunned and removed from an electric field was 20 min for exponential (capacitor or condenser-discharge) PDC, 60 min for DC, and 120 min for AC. However, full physiological recovery can require more than 6 h for electrofished rainbow trout (Schreck et al., 1976) or 24 h or longer for other species (Whaley et al., 1978; Barton and Dwyer, 1997). Some species are so sensitive to certain stresses that recovery can take weeks or months (e.g., handling and confinement stresses in some sharks–Smith, 1991). Stress can be so great, or fish so sensitive, that some fish eventually die. Because of the effects of electrofishing on blood chemistry, the U.S. Environmental Protection Agency recommended that electrofished specimens not be used in physiological or bioassay studies (Weber, 1973, according to Emery, 1984).

In response to tetany in a DC field, Schreck et al. (1976) reported immediate increases in blood concentrations of plasma corticoid (adrenal hormones, steroids), lactate or lactic acid (by-product of anaerobic muscular activity), and thrombocytes (white blood cells instrumental in blood clotting) in yearling, hatchery-reared rainbow trout. Increases in thrombocytes might be at least partially a response to tissue trauma, minor bleeding, or

hemorrhage. Blood glucose exhibited a delayed response, not increasing significantly until after lactic acid levels returned to normal, about 3 h after being tetanized. Schreck et al. (1976) found no immediate effect on blood levels of packed cells (hematocrit), plasma protein, calcium, magnesium, or androgen, nor did they find any effect on electrophoretic patterns of 13 tested isoenzyme systems (proteins often used in systematic analyses).

Other biologists also reported rapid increases in plasma cortisol in shocked fish. For rainbow trout ($\bar{x}$ = 113 g) exposed to 20 s of homogeneous 60-Hz PDC (240–270 µS/cm; 16° C), Mitton and McDonald (1994a) found that plasma cortisol increased more than two-fold and lactate about six-fold within the first 1 h then returned to near resting levels by 8 h and 4 h, respectively, after exposure. Maule and Mesa (1994) exposed juvenile chinook salmon ($\bar{x}$ = 8 g, 9 cm FL) to 1.5 s of 120-Hz PDC (73 µS/cm; 13° C) and reported that plasma cortisol remained the same in survivors (16% and 25% mortality in test tanks) as in controls for fish sampled within 4 s of exposure but, as reported by Schreck et al. (1976) and Mitton and McDonald (1994a), rose rapidly within the next 15 min, continued to rise to a peak (four to five-fold) by 1 h after treatment, then declined gradually to control levels by 6 h. Barton and Dwyer (1997) also reported an increase in plasma cortisol to a peak during the first hour, but the increase was greater than ten-fold for juvenile bull trout subjected to 10 s of either 60-Hz PDC at a lethal field intensity (calculated as possibly 2.8 V_p/cm; ambient conductivity 219 µS/cm; 9° C) or 60-Hz PDC or DC at a lower, non-lethal intensity (possibly 1.3 or 1.4 V_p/cm). Fish subjected to the non-lethal fields recovered from narcosis within about 1 min and showed no external signs of injury (Barton, personal communication) but required at least 24 h for plasma cortisol levels to gradually return to pre-shock levels, a much longer time than reported by Maule and Mesa (1994) and Mitton and McDonald (1994a).

Like Schreck et al. (1976), Mitton and McDonald (1994a) also reported that plasma glucose rose more slowly and less extensively (60% increase) to a peak about 4 h after treatment, then gradually returned to resting levels in 8 h. Unlike Schreck et al. (1976) and Mitton and McDonald (1994a), Barton and Dwyer (1997) found that plasma glucose in shocked fish rose immediately (within the first hour) to about twice pre-shock levels, then remained at that raised level for the remainder of a 24-h monitoring period.

Other physiological indicators of stress also have been investigated. Mitton and McDonald (1994a) reported immediate increases in catecholamines (greater than three-fold from non-detectable levels), metabolic acid, and carbon dioxide (about two-fold) and a decrease in pH (more than 0.2 units). Catecholamines and carbon dioxide returned to resting levels within an hour or two, whereas metabolic acid and pH overshot their return to resting levels within that time but stabilized back to near resting levels within 8 h after treatment. Burns and Lantz (1978) reported results similar to those of Schreck et al. (1976) for lactate, hematocrit, and plasma protein in adult largemouth bass. They also tested electrofishing effects on hemoglobin concentrations in the blood and the percentage of water in muscle tissue but found no differences from control fish or changes during a 19-h period after electrofishing. Contrary to the findings of Burns and Lantz (1978) and Schreck et al. (1976), Bouck and Ball (1966) reported changes in plasma protein concentrations (and composition) in rainbow trout captured by electrofishing, as well as by seining and hook-and-line fishing.

Based on significantly lower levels of plasma cortisol and glucose in juvenile bull trout subjected to handling stress (30 s aerial exposures in a dip net) and controls that were transferred between tanks, Barton and Dwyer (1997) concluded that the physiological stresses of DC and 60-Hz PDC electrofishing are significantly greater than handling stresses. Mitton and McDonald (1994a) compared the physiological effects of combined electroshock and 1 min of aerial exposure with electroshock only for rainbow trout and reported similar elevations of cortisol and glucose; significant increase in catecholamines; non-significant increases in lactate, carbon dioxide, and metabolic acids; and decrease in pH. In another experiment, they monitored survival of rainbow trout exposed to the combined stress of 20 s of 60-Hz PDC and up to 4 min aerial exposure and reported no fatalities during the next 2 weeks.

All capture methods are stressful to some degree (Wydoski, 1980). Schreck et al. (1976) concluded that stress induced by electrofishing is similar to that caused by hypoxia and extreme muscular activity. Similarly, Mitton and McDonald (1994a) emphasized that in salmonids, stress response to electrofishing is comparable in magnitude to other acute stressors such as handling and exhaustive exercise, including those resulting from capture by angling. On the other hand, and as noted above, Barton and Dwyer (1997) found the stress caused by electrofishing to be significantly greater than handling stress. Stresses can be cumulative; electrofishing stresses added to existing environmental stresses (e.g., pollution) can increase mortality significantly over either alone (Wydoski, 1980). Increased mortality can occur directly as a result of stress and fatigue or indirectly through greater susceptibility to predators, disease, and parasites. In some cases, delayed, stress-related mortality may be more significant than immediate electrofishing mortality. Injury-related stresses may persist and affect the fish's physiology, behavior, growth, and reproduction for a long time.

Mortality, stress, and some injuries can result as much from poor, improper, or careless handling after capture as from electrofishing itself (Hudy, 1985; Barrett and Grossman, 1988). Because stress can also be induced by confinement, fish not being held for longer-term observation should be released as soon as possible after recovering equilibrium and normal respiration. Earlier release might make them especially easy prey for predators (Whaley, 1975; Whaley et al., 1978). Waiting until equilibrium and respiration are adequately reestablished also allows more opportunity to observe, document, and aid injured or distressed specimens. If undesirable effects are observed, electrofishing procedures should be adjusted to minimize those effects. Emery (1984) suggested adding salt (1.5%) and a light anesthetic to the holding water to help fish replace lost ions and reduce additional stress. However, if the anesthetic slows recovery of respiration in fish that have been tetanized, it might do more harm than good. Eloranta (1990) reported that recovery of electrofished specimens was slower and mortality (70–80%) significantly higher in unaerated containers treated with MS-222 (tricaine methanesulfonate) than in containers without the anesthetic.

Electrofishing also affects subsequent fish behavior. Mesa and Schreck (1989) observed that rates of feeding and aggression decreased in hatchery-reared and wild cutthroat trout immediately after the they were electrofished and marked in an artificial stream. In a natural stream, they reported that similarly electrofished and marked wild trout immediately sought cover, remained relatively inactive, did not feed, and were easily approached by a diver. An average of 3 to 4 h was required for 50% of the fish to return to normal behavior. In contrast, fish that remained uncaptured in the same section of the stream, even after successive passes, exhibited little change in normal behavior. Either uncaptured fish were insufficiently affected by the electric fields, or handling and marking of captured fish were responsible for differences in behavior. Callahan (1996) reported reduced feeding by large and small bluegill for up to 5 h after being electrofished. In associated predator experiments in a 2.4 m diameter pool, he found small bluegill more likely to be eaten by largemouth bass immediately after being shocked than unshocked bluegill but that differences in susceptibility to predation decreased with time and after 10 min shocked bluegill recovered sufficiently to behave like unshocked bluegill. However, Callahan suggested that these temporary effects on feeding and susceptibility to predation would have a negligible effect on a population. Horak and Klein (1967) experimented with rainbow trout and found that swimming performance was significantly reduced in fish captured by electrofishing. For juvenile rainbow trout (3–12 g, 6–12 cm) exposed to 20 s of 60-Hz PDC, Mitton and McDonald (1994b) reported that the reduction in swimming performance was comparable to that for fish forced to exercise for 5 min. Swimming performance in both shocked and exercised fish dropped gradually for 1 h after treatment to 53% of control values then recovered to near control performance within 2 to 4 h of treatment. Swimming performance deceased beyond that of exercised fish when shocked fish were subsequently exposed to air for 1 to 4 min; those fish exposed to air for 4 min experienced a 62% drop in swimming performance between 0.5 and 1 h after treatment and required more than 6 h for recovery of normal endurance. Fatigue from long exposure or high-intensity fields can also reduce a fish's short-term sensitivity to subsequent exposures (Chmielewski et al., 1973). Cross and Stott (1975) suggested that electrofished specimens might be less catchable for the next 3 to 24 h and that this response could substantially affect population estimates based on short-term mark-recapture or depletion techniques.

Spinal and Related Injuries

Hauck (1949) provided perhaps the most detailed description of electrofishing injuries. In a rescue attempt, 503 rainbow trout (0.7–2.3 kg), were electrofished from a canal (14–21° C) in Idaho using hand-held electrodes and a portable (truck-mounted), 110-V, 60-Hz, 495-W AC generator. Voltage was set by rheostat at 80 to 90 V, just enough to momentarily stun fish within 3 m of the electrodes. Hauck (1949) noted that reactions of fish in the field varied. Respiratory activity increased in all fish, and most fish experienced at least partial muscular paralysis. Fish exhibiting partial paralysis swam in an arc around the electrode (oscillotaxis), whereas those exhibiting total paralysis (probably tetany, including cessation of respiratory movements) would float momentarily on their sides then sink slowly to the bottom.

Hauck (1949) described the injuries in captured fish as follows: "A number of fish hemorrhaged from the gills or vent, or both. Others showed dilated and hemorrhaged blood vessels in the skin near the vent. Several were observed with the intestine protruding from the vent. Physical contact with the electrode caused the appearance of dark vertical bars on that area of the fish which touched the electrode."

The fish were transported to a nearby hatchery pond where they were observed for 2 to 5 days before release. During this time, 131 fish (26%) died either as a result of electrofishing or subsequent handling. Although not stated, incidence of injury was probably much higher than mortality (Reynolds and Kolz in Reynolds et al., 1988). Hauck (1949) noted that "Paralysis of swimming muscles persisted in some fish for several days. This loss, or partial loss, of locomotion would indicate an injury to the nervous

system. The dark, vertical bars remained in evidence. Dead or dying tissues in the caudal peduncle and caudal fin appeared on several fish which fact would indicate loss or impairment of circulation to this region. Several fish lost their sense of balance."

Hauck (1949) dissected 10 specimens with representative injuries from among the rescued fish. "One 5-pound rainbow trout had a fractured sixth caudal vertebra. As a result of this fracture the haemal artery and vein had ruptured in the seventh caudal vertebra. The breakdown of circulation of blood at this point caused the death of the entire body posterior to the injury, including muscles and skin. Blood clots and hemorrhaging were evident throughout the caudal peduncle, particularly in the region adjacent to the fracture. This fish suffered total paralysis of the swimming musculature before its death."

"A 1.5-pound specimen had three fractured vertebrae, the 11th, 29th, and 30th abdominals. Curvature of the spine appeared through the abdominal vertebrae 18 to 22, and the ligamentous connections between ribs and parapophyses in this region were broken. This fish also had blood clots in the afferent branchial arteries and had hemorrhaged through the membranes of the gill filaments."

He described 4 more of the 10 fish as having fractured vertebrae or spinal curvature, which he described as ligamentous fractures. One of these fish had 12 ruptured dorsal (probably segmental) arteries anterior to a fracture in a single abdominal vertebra. Another, that had an impaired sense of balance before it was killed, had bloody fluid in the semicircular canals. Six of the 10 fish suffered injury in the region of the brain, as evidenced by dilated blood vessels or blood clots. Hauck (1949) suggested that the latter brain injuries might have been secondary to electrofishing, perhaps caused by collisions with rocks or other structures. He concluded his 1949 publication with the suggestion that further investigations on the injurious effects of electrofishing were needed before the technique was widely employed in fishery management.

Nature of the Injuries

Compressed, broken, or misaligned vertebrae and related electrofishing injuries, including separated or damaged ribs, damaged swim bladders, ruptured dorsal and haemal arteries, and other internal hemorrhages (Figs. 16–18), are believed to be caused by momentary but powerful convulsions of the body musculature. Bleeding at the vent could be caused by related damage to the viscera, but bleeding at the gills is probably a separate phenomenon. Lamarque (1990) suggested that such convulsions are the result of direct excitation of the muscles (perhaps via motor nerves) and "hyper-reflexivity." Sharber et al. (1994, 1995) and Sharber and Black (1999) surmised that these convulsions or myoclonic jerks are random seizures similar to those sometimes experienced by people with epilepsy or subjected to electroconvulsive therapy before chemicals were available to block stimulation of motor neurons.

Myoclonic jerks or seizures are thought to occur simultaneously, or nearly so, on both sides of the body, thereby subjecting the vertebral column to opposing forces that can break, crush, or dislocate the vertebrae (Lamarque, 1990; Sharber et al., 1994; Sharber and Black, 1999; Figs. 16 and 18). Stewart (1967; according to Lamarque, 1990) reported that spinal injuries by DC (perhaps actually PDC) are primarily compression fractures, whereas those produced by AC are primarily misalignments. However, Hollender and Carline (1994) reported that among brook trout electrofished with 250 to 300-Hz AC or 60-Hz PDC, the frequency of compression-only injuries was greater in AC, whereas the frequencies of fractures, complete separation of vertebrae, and combinations of vertebral misalignments and compressions were similar in both types of current. Using PDC, Sharber and Carothers (1988, 1990) and Fredenberg (1992) observed both compression fractures and misalignments. Comparing DC and several PDCs, Fredenberg (1992) concluded that there were no notable differences in the types of injuries caused by the various currents, only differences in their frequency and severity; he particularly noted that misalignments were relatively rare in DC. Like Fredenberg (1992), Dalbey (1994) and Dalbey et al. (1996) reported substantially greater incidences of spinal injury among rainbow trout captured with PDC (54%) or a hybrid of PDC over DC (40%, Fig. 5J) than with DC (12%), but most of the differences were manifest in a substantially greater percentage of fish having less severe spinal damage (compression between vertebrae and misalignment) when exposed to PDC or the hybrid current (44% and 34%, respectively, vs. 6% for DC). As a result, the percentages of fish afflicted with the most severe spinal damage (fractures of vertebrae, Fig. 18, or complete separation of two or more vertebrae, Fig. 16) were similar for all three currents (6–10%).

Electrofishing-induced vertebral damage is usually accompanied by ruptured blood vessels, torn muscles or ligaments, and perhaps other soft-tissue damage (Fig. 17; Hauck, 1949; Taylor et al., 1957; Spencer, 1967a; Sharber and Carothers, 1988, 1990; Holmes et al., 1990; Wyoming Game and Fish Department, 1990; Fredenberg, 1992). However, Holmes et al. (1990), Fredenberg (1992), and others also observed hemorrhages along the spine or in the musculature without apparent corresponding damage to vertebrae. Sometimes the incidence of such hemorrhages was much greater than the incidence of obvious vertebral damage. Grisak (1996) found that the

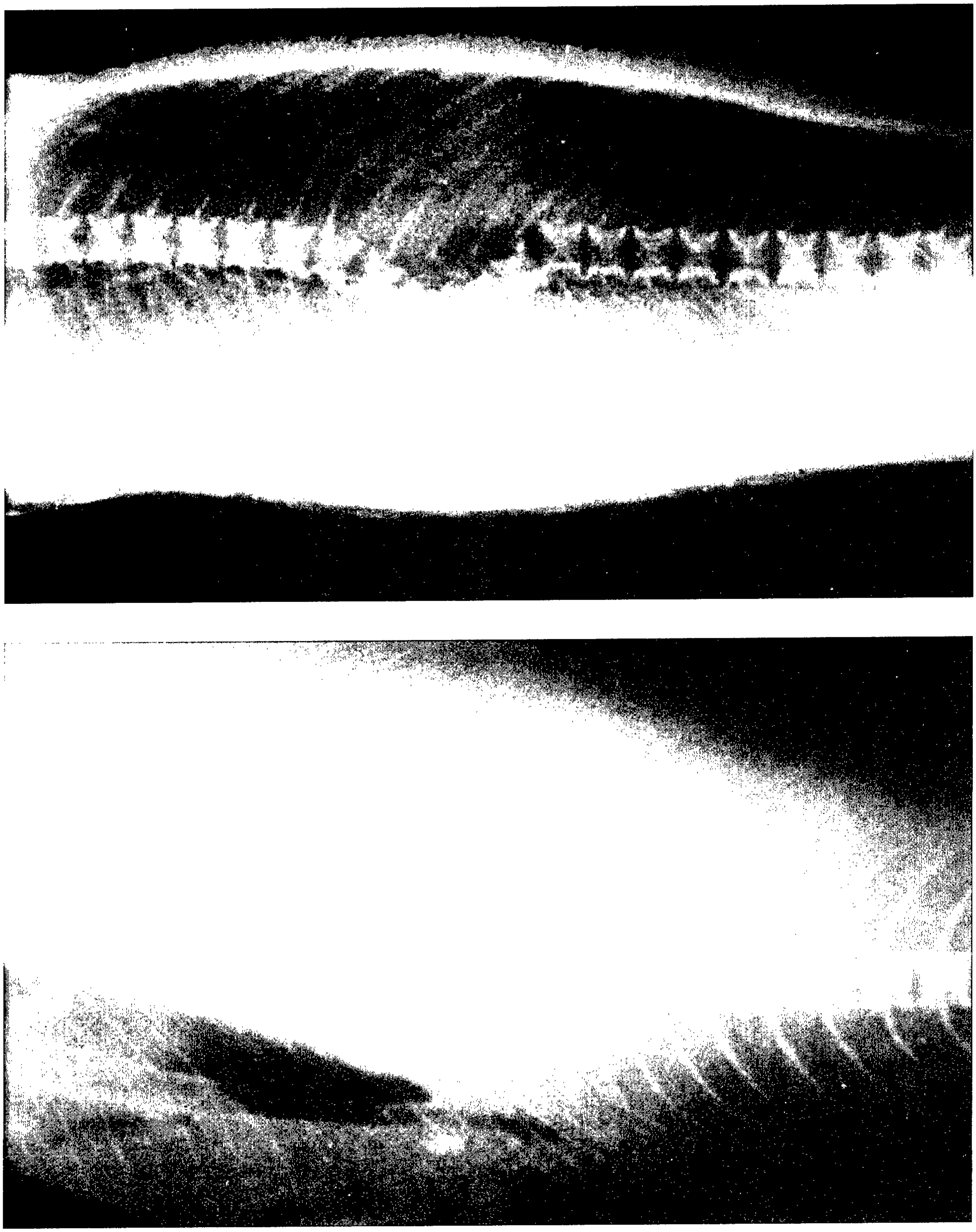

Fig. 16. Dorsal- (top) and lateral-view (bottom) X-rays of a rainbow trout (*Oncorhynchus mykiss*) revealing spinal misalignment and fractured vertebrae caused by electrofishing. (Photographs provided by and reproduced with the permission of N.G. Sharber, Coffelt Manufacturing, Inc., Flagstaff, Arizona.)

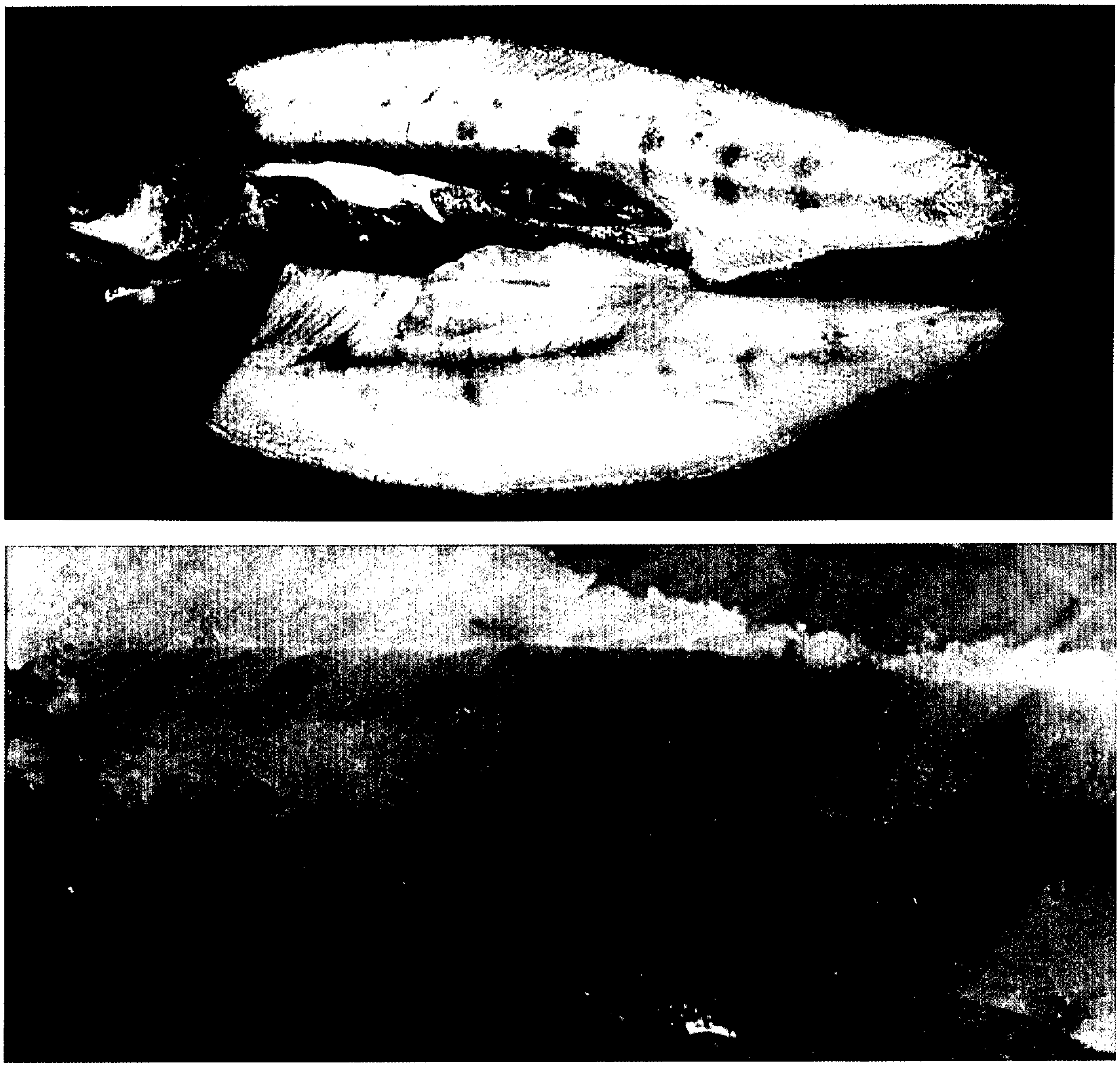

Fig. 17. Necropsy fillets of rainbow trout (*Oncorhynchus mykiss*) revealing hemorrhages and associated tissue and vertebral damage caused by electrofishing, top showing multiple injuries. (Photographs provided by and reproduced with the permission of N.G. Sharber, Coffelt Manufacturing, Inc., Flagstaff, Arizona.)

relative incidence of vertebral damage and muscular hemorrhages varied among species and with different electrical currents. For goldeye collected by DC, he reported incidences of 21% for each type of injury, but for goldeye taken by 40-Hz PDC, he reported only 4% with spinal damage and a high of 39% with hemorrhages. All but two goldeye had only muscular hemorrhages (all class 1 or 2—Table 3) or only vertebral damage (nearly all class 1). Among other species injured with 40-Hz PDC, Grisak (1996) reported that all flathead chub injuries were spinal damage (8%) and that twice as many river carpsucker injuries were spinal damage (18%) than hemorrhages (9%). Among controls also X-rayed and necropsied (105 fish collected with other sampling gear), Grisak (1996) reported only one fish (a goldeye) with a fresh internal injury, a spinal compression (class 1). Ruppert (1996) and Ruppert and Muth (1997), subjected juvenile humpback chub and bonytail (5–10 cm TL; n = 390) to a variety of PDCs at thresholds for taxis, narcosis and taxis, and reported hemorrhages associated with the spine in 13% of the fish (up to 27% for individual treatment means) but no apparent vertebral damage; only one of 120 control fish suffered an internal hemorrhage. To a lesser extent, the reverse situation, vertebral damage

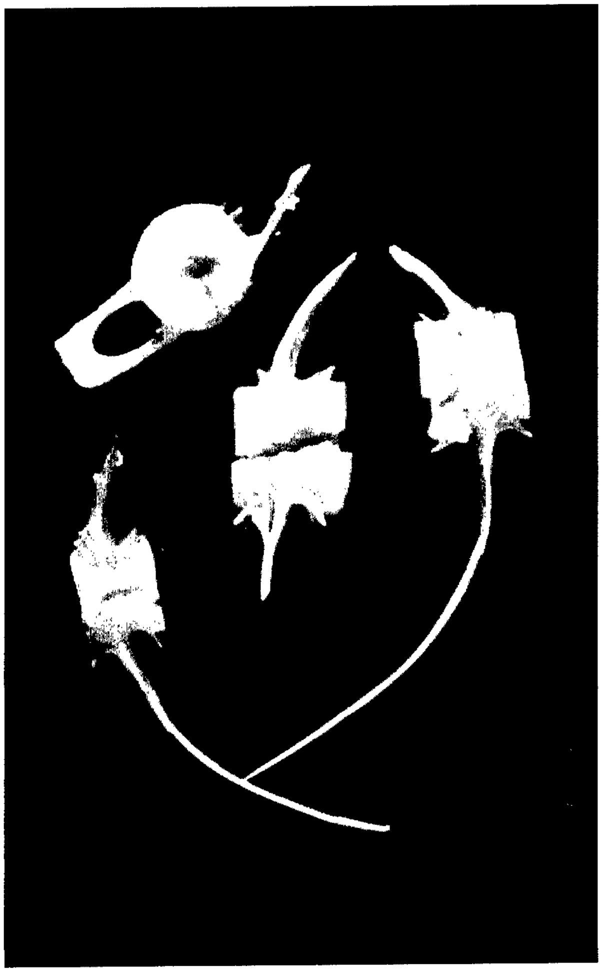

Fig. 18. Fractured vertebrae from a rainbow trout (*Oncorhynchus mykiss*) caused by electrofishing. (Photograph provided by and reproduced with the permission of W.A. Fredenberg, Montana Department of Fish, Wildlife, and Parks.)

without associated hemorrhages, has been observed in other studies. Among brook trout subjected to AC or PDC, Hollender and Carline (1994) reported two to three times more incidences of spinal damage without hemorrhages (16% for AC, 11% for PDC) or hemorrhages without vertebral damage (10% for AC and PDC) than incidences of both in the same fish (5% for AC, 4% for PDC). Fredenberg (1992) observed that when only hemorrhages or damaged vertebrae were detected, the injuries were usually minor to moderate, but Hollender and Carline (1994) found most such injuries to be moderate to severe.

Electrofishing-induced spinal injuries can occur anywhere along the spinal column, including immediately behind the head, but most have been observed near or posterior to the middle of the spine. Predominant location varies with species. Spinal injuries in Salmoninae are most frequently located near or between the dorsal or pelvic fins and the anal fin (Sharber and Carothers, 1988, 1990; Meyer and Miller, unpublished manuscript, 1991; Fredenberg, 1992; Hollender and Carline, 1994; Kocovsky et al., 1997), whereas those in centrarchids and ictalurids are predominantly located in the caudal region, posterior to the vent (Spencer, 1967a). Among ripe razorback sucker (an endangered species) experimentally shocked by Muth and Ruppert (1996), most injured fish had spinal hemorrhages near the origin of the dorsal fin. The only fish with an obviously damaged spine had two vertebral injuries (class 2 and 3) with associated hemorrhages, one located just posterior to the dorsal fin and the other slightly behind the anal fin. Ruppert and Muth (1997) reported that most spinal hemorrhages observed in humpback chub and bonytail were located between the dorsal and caudal fins. Grisak (1996) reported most spinal damage and hemorrhages for goldeye and cypriniform fishes taken in the Missouri River occurred in the middle and posterior portions of the body.

The number of vertebrae involved in each incident of spinal damage varies considerably, from one to as many as 20, depending on species and severity of the injury. For example, Hollender and Carline (1994) reported that most spinal injuries in brook trout subjected to AC or PDC involved five to seven vertebrae with an extreme range of two to 18. Spinal dislocations, fractures, or both reported for large rainbow trout by Sharber and Carothers (1988, 1990) involved a mean of eight vertebrae. For warmwater fishes, Grisak (1996) reported that most spinal injuries involved three to nine vertebrae. Fredenberg (1992) found that misalignments in trout typically involved two to five vertebrae among a larger series of compressed vertebrae.

Multiple injuries, especially spinal hemorrhages, are quite common (Fig. 17 top). Ruppert and Muth (1997) reported a mean of three and up to eight hemorrhages for individual juvenile humpback chub and bonytail injured by electric fields. Over 60% of injured trout examined by Fredenberg (1992) and his associates were characterized by two or more hemorrhages, with up to eight in one specimen; multiple, well-spaced vertebral injuries were also common. Among electrofished rainbow and brown trout X-rayed by Meyer and Miller (1990), up to 41% (50% of injured fish) experienced two spinal injuries and up to 11% (14% of injured fish) had three injuries. However, in the next year they successfully X-rayed 220 electrofished trout and observed spinal injuries in 17% of those trout but only one fish with multiple injuries (Wyoming Fish and Game Department, 1991). For annually electrofished salmonids examined by X-ray and found to have either old (healed) or new spinal injuries or both,

Table 3. Procedures and criteria for documenting damage to fish spinal columns and associated hemorrhages. From Box 8.2 in Reynolds, 1996.

Procedures	Criteria
Spinal damage	
Fish should be dead or anesthetized to insure good resolution on X-ray negatives. Photograph (X-ray) the left side of each fish, positioning it to include all vertebrae. Photographs (X-rays) from the dorsal aspect also may be necessary to clarify the injury rating. X-rays of two or more fish per plate will save money. Record the position of every affected vertebra, counting the first separate vertebra behind the head as number 1. Rate the worst damage to the spine.	0 - No spinal damage apparent 1 - Compression (distortion) of vertebrae only 2 - Misalignment of vetebrae, including compression 3 - Fractures of one or more vetebrae or complete separation of two or more vertebrae
Internal hemorrhage	
Fish should be killed within 1 h after capture and either frozen or held on ice to allow clotting in blood vessels. Fish should not be filleted immediately after death because fillet-related bleeding will mask injury-related hemorrhages. Fillets should be smoothly cut close to rays and spine and through the ribs and back to the caudal peduncle. Rate the injury from the actual specimen, then photograph the worst side of fish with the fillet inside up (color slides are best for follow-up evaluation). Rate the worst hemorrhage in the muscle mass.	0 - No hemorrhage apparent 1 - Mild hemorrhage; one or more wounds in the muscle, separate from the spine 2 - Moderate hemorrhage; one or more small wounds on the spine ($\leq$ width of two vertebrae) 3 - Severe hemorrhage; one or more large wounds on the spine (> of two vertebrae)

Kocovsky et al. (1997) reported that 77% had one injury, 17% had two injuries, and 6% had three injuries (also that 56% were class 1 injuries, 19% class 2, and 25% class 3). Some of the multiple injuries they reported had accumulated from prior years of electrofishing.

Fredenberg observed that multiple hemorrhages frequently alternated from side to side, sometimes in evenly spaced patterns. Explanations for multiple hemorrhages occurring on only one side or alternating side to side, have yet to be studied. If multiple injuries are the result of multiple, temporally separated seizures and all myomeres contract simultaneously, it would be logical to expect that the weakest portion of the spine (that which is already injured) would be most susceptible to subsequent injury. However, multiple injuries at different locations might be likely if the nerves associated with the original injury were also damaged or otherwise made, at least temporarily, nonfunctional (i.e., no longer subject to stimulation or overstimulation). Alternating side-to-side hemorrhages might be the result of successive convulsions as the fish bend from side to side during taxis towards the anode. If multiple injuries result from single convulsive events, perhaps the muscular contractions sometimes differ in strength or intensity on each side of the body or in different regions of the body.

Detection and Evaluation of the Injuries

Participants in a special session on electrofishing injuries, held at the June 1991 meeting of the Western Division of the American Fisheries Society (Bozeman, Montana), considered, modified, and agreed on a set of procedures and criteria recommended by J. B. Reynolds for standard documentation of the presence and severity of damage to the spine and associated hemorrhages (Table 3). These procedures and criteria have since been detailed in many publications, including Reynolds (1996). By these criteria, vertebral damage (usually based on X-rays) and hemorrhages (based on clean fillets of muscle tissue along the spine) are separately ranked from zero to three according to severity. Since its introduction, this severity rating system for spinal injuries and hemorrhages has been used by many biologists (e.g., Roach, 1992; Taube, 1992; Dalbey, 1994; Hollender and Carline, 1994;

Thompson, 1995; Ruppert and Muth, 1997). Fredenberg (1992) used the criteria and reported that despite cases in which hemorrhages were observed without corresponding identification of vertebral damage, and vice versa, severity ratings for damage to the spine and hemorrhages in associated tissues were reasonably similar, and severe injuries were nearly always detected as such by both criteria. Although the procedures originally recommended by Reynolds specified only lateral-view X-rays, Thompson et al. (1997a) suggested use of dorsal- as well as lateral-view X-rays to facilitate interpretation of the nature and severity of spinal injuries (Fig. 16). Fredenberg (1992) observed that less severe hemorrhages are often only visible on one side of the spine and suggested that necropsy procedures should include fillets of both sides.

Bent or curved backs, bleeding, or brands may be obvious signs of internal injuries, but such external signs of spinal and related internal injuries are often absent. Injured fish often look fine and appear to behave normally. When external manifestations of present or past (healed) injuries are present, they usually indicate that internal injuries are or were relatively severe (Kocovsky et al., 1997).

Brands, sometimes referred to as bruises or burn marks, are particularly obvious indications of injury (Fig. 2). They can result from direct contact with or proximity to the electrode, but also appear on fish netted some distance from an electrode (Lamarque, 1990). Although Lamarque (1990) noted that some brands may be true burns from direct contact with an electrode, he, Emery (1984), Fredenberg (1992), and Sharber and Black (1999) suggested that most brands are discolorations of the skin due to the dilation of skin melanophores, possibly as a result of sympathetic nerve damage or stimulation. Reynolds (1996) agreed that at least blotchy, irregular-shaped marks are probably temporary intensifications of dermal pigment, but suggested that some dark marks, particularly the anterior-pointing chevron-shaped marks, are hemorrhages in or under the skin caused by ruptured capillaries. Blood also might seep from deep internal hemorrhages along myosepta and appear under the skin. Over 30 years ago, Horak and Klein (1967) recognized internal hemorrhages and possible vertebral injuries as a cause for such marks. Lamarque (1990) suggested that if a large part of the body became dark, a total rupture of the spinal column was probable. Although marks resulting from hemorrhages under the skin are best described as bruises, the term brand is more widely accepted to cover dark discolorations regardless of cause and is used accordingly in this report.

Most brands, especially pigmental brands, tend to be ephemeral. They rapidly dissipate after death (Fredenberg, 1992) and vanish within 4 days, perhaps much sooner, on living specimens (Holmes et al., 1990). However, Hudy (1985) observed brands, probably resulting from hemorrhages, remaining on some fish for 15 days after they were electrofished.

Brands, especially those resulting from subdermal hemorrhage, effectively approximate the location of damaged vertebrae or associated tissues (Lamarque, 1990; Fredenberg, 1992), but their absence does not indicate a lack of spinal injuries. In one sample of 152 electrofished rainbow trout, Fredenberg (1992) reported that 26% had brands, and all but one of those branded fish were found upon X-ray analysis or necropsy to have associated spinal injuries. However, among the unbranded fish in the sample, another 37% were determined to have spinal or related tissue damage, bringing the total with such injuries to 63%. Among injured fish, the incidence of severe injuries was much greater among branded than unbranded fish (64% vs. 17%). Horak and Klein (1967) found brands on 39% of the hatchery-reared rainbow trout they electrofished; extrapolating from Fredenberg's (1992) observations, many more of their fish probably had spinal injures. Krueger (personal communication) observed that over 50% of rainbow trout and brown trout that he electrofished for contaminants analysis had brands posterior to the dorsal fin. Many of the trout he subsequently dissected had damaged spinal columns, and most of these also had brands. McMichael and Olson (unpublished manuscript, 1991) also reported a positive relation between the incidence of brands and spinal injuries for hatchery rainbow trout subjected to electrofishing fields.

Except when particularly severe, recent spinal and related internal injuries often can only be detected or positively verified by X-ray and necropsy (Sharber and Carothers, 1988, 1990). Although Grisak (1966) reported up to 43% spinal injuries (class 1 only) or hemorrhages (class 1 and 2) among electrofished non-salmonid fishes based on X-rays and necropsy, he observed no brands, even though all were reportedly tetanized and some had been in contact with the anode. Kocovsky et al. (1997) found accumulated incidences of externally detectable spinal injuries (old, healed injuries) in up to 23% of salmonids sampled annually by electrofishing, but also found upon X-ray examination that nearly half (44%) of the fish without external signs of injury also had spinal injuries. Although Fredenberg (personal communication to McMichael, 1993) suggested that necropsies may be up to a third less effective than X-rays for detection of less-severe or less-obvious vertebral damage, necropsies may be necessary to support or help interpret X-ray analyses. Necropsies are also necessary to detect soft-tissue injury and hemorrhages, which, as discussed earlier, might or might not be directly associated with obvious spinal damage. Hollender and Carline (1994) concluded

that accurate assessment of spinal injuries and muscular hemorrhages should be based on both X-rays and necropsy.

Based on their own experiments and observations, McCrimmon and Bidgood (1965) stated that unless X-rays are also taken prior to electric-field exposure, vertebral damage caused by electric fields might be difficult to distinguish from previous anomalies. They documented such prior anomalies in up to 16% of rainbow trout electrofished from Great Lakes tributaries in Ontario. All anomalies were compacted segments of the spine usually involving four to nine vertebrae between the dorsal and pelvic fins, but no significant curvature or misalignment was noted. The affected vertebrae were typically 60 to 75% shorter than normal vertebrae and, at least in fish that were dissected, fused and immobile. Sharber and Carothers (1988) stated that McCrimmon and Bidgood (1965) could not determine the cause of the abnormalities, but McCrimmon and Bidgood (1965) had concluded that these anomalies were probably of natural origin (genetic or developmental) and definitely not electrofishing injuries.

Other researchers have also documented the incidence of natural or non-electrofishing spinal injuries or anomalies. Gill and Fisk (1966) X-rayed nearly 20,000 fish and documented "natural" (genetic or environmental) vertebral abnormalities in 0 to 11% of the fish in samples of wild adult pink, sockeye, and chum salmon. Gabriel (1944, as cited by McCrimmon and Bidgood, 1965) similarly documented vertebral abnormalities in 2 to 3% of mummichog examined from natural populations. As in McCrimmon and Bidgood's (1965) trout, most of these abnormalities were compressed and fused vertebrae; misalignments, if any, were not reported. Zeigenfuss (1995) X-rayed 209 wild salmonids ($\bar{x}$ = 21–32 cm TL) that were trapped from three Colorado reservoirs and presumably never exposed to electrofishing fields. He observed spinal anomalies in 72% of brook trout from one high mountain reservoir, in 6% of brook trout and 14% of rainbow trout from another reservoir, and in none of kokanee from the third reservoir. Zeigenfuss (1995) described the anomalies as mostly severe spinal compressions (probably similar to that illustrated in Fig. 19A). Meismer (1999) found that many hatchery rainbow trout used to assess injurious effects of electric fields had externally obvious shortened caudal peduncles caused by compression and fusion of several caudal vertebrae. These anomalies, which he suspected to be congenital defects, included a covering of calcified tissue and were readily distinguishable from new electrical-field injuries.

The distinction between natural spinal anomalies and old and new spinal injuries can sometimes be disturbingly subjective. Sharber and Carothers (1988, 1990) observed that naturally occurring (e.g., genetic, developmental) spinal anomalies appeared dense (compressed) and fused in X-rays and that electrofishing-induced damage was distinguished by separation or notable misalignment of vertebrae. They also implied, with photographs of X-rays (reproduced here as Fig. 19), that old injuries could be distinguished from natural anomalies and recent injuries but did not discuss criteria. Fredenberg (1992), Dalbey et al. (1996) and Thompson et al. (1997a) more specifically noted that in X-rays, old electrofishing injuries were evidenced by heavy calcification and fusion and, as suggested by Sharber and Carothers (1988, 1990), were usually distinguished by vertebral misalignment from natural anomalies. However, electrofishing induced injuries usually include, and are often predominated by, compressions of the spine without misalignment (designated as class 1 injuries) and in these cases may be particularly difficult to distinguish from similar-appearing, old or new injuries or anomalies by other causes.

Despite difficulties in distinguishing between some natural spinal anomalies and old and new spinal injuries, such determinations are critical to interpretation of the results of an investigation. For fish electrofished (60-Hz, half-sine PDC) from three Colorado Rivers and examined by X-rays, Thompson et al. (1997a) reported frequencies of 9 to 19% for old vertebral injuries and genetic abnormalities among rainbow trout and 8 to 33% among brown trout versus frequencies of 6 to 64% and 18 to 52%, respectively, for new spinal injuries. Among X-rayed and necropsied fishes collected from the Missouri River, Montana, by electrofishing and other techniques, Grisak (1996) reported that 4% of goldeye, 3% of flathead chub, 24% of river carpsucker, 6% of shorthead redhorse, and 11% of longnose sucker had spinal anomalies that he attributed to congenital deformities or old injuries. Based on close external examination, Kocovsky et al. (1997) assessed the accumulation of old spinal injuries among three salmonids and longnose sucker electrofished annually from three Colorado streams. For the salmonids, they reported annual increases in injury incidences with cumulative totals up to 23%. For longnose sucker, incidences of externally detected spinal injuries ranged up to 13% but varied among years suggesting a notable change or turnover in the population rather than progressive accumulation of electrofishing injuries.

Interpretation of the nature and cause of spinal anomalies or injuries must be made with care. As documented by Gabriel (1944, as cited by McCrimmon and Bidgood, 1965), McCrimmon and Bidgood (1965), and Gill and Fisk (1966), natural occurrences of spinal anomalies, especially compressions, may be common in some wild or cultured populations. Also, lordosis (dorsoventral bends or misalignments), scoliosis (lateral bends or misalignments), or vertebral compressions can result

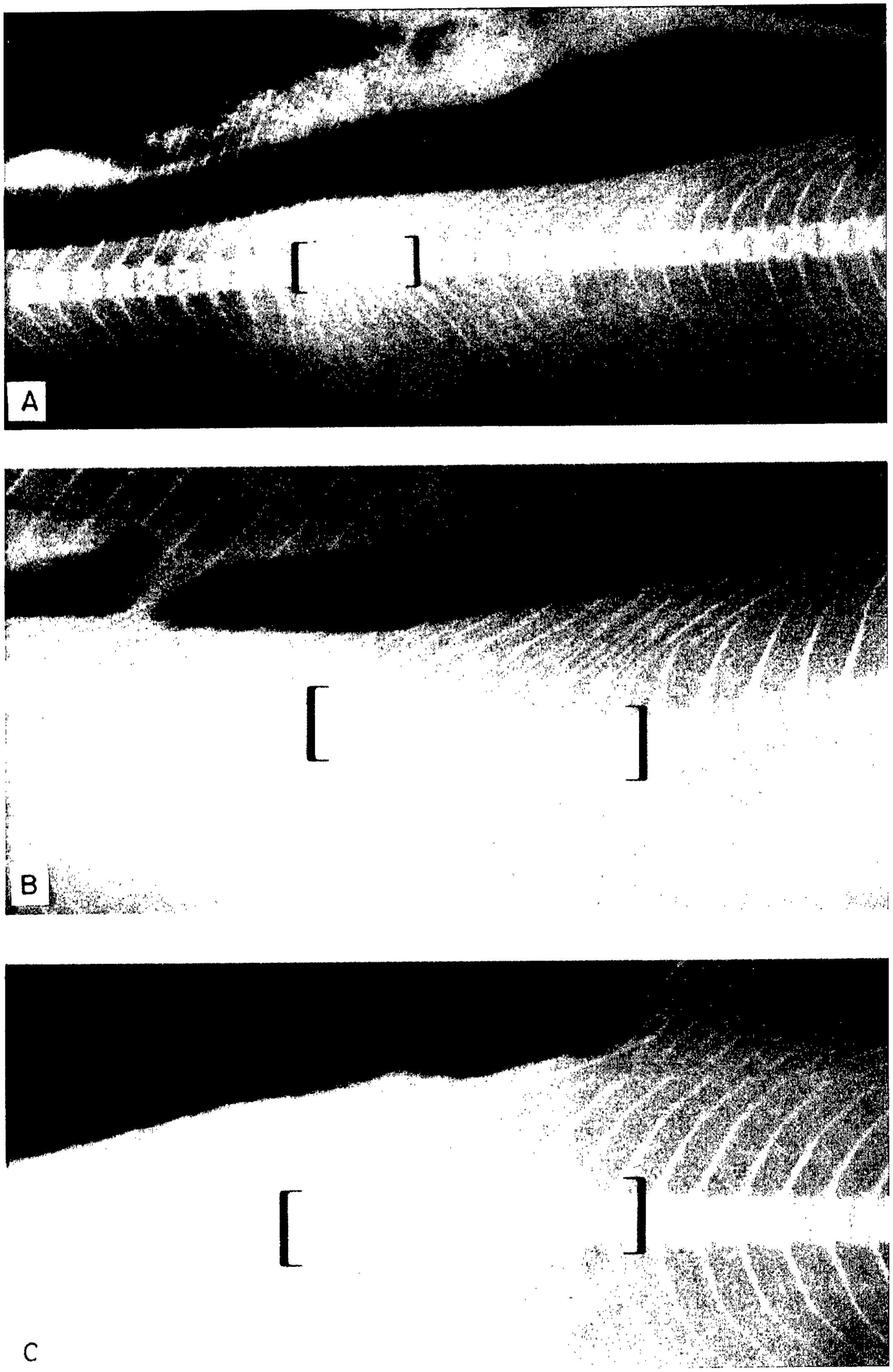

Fig. 19. X-rays of a natural spinal anomaly (A), an old spinal injury (B), and a recent electrofishing-caused spinal injury (C) in rainbow trout (*Oncorhynchus mykiss*). (Reproduced with permission from Fig. 1 in Sharber and Carothers, 1988.)

from abnormal development, nutritional deficiencies, pollutants, or injury caused by accidents, parasites, or predators.

Spinal injuries also can be caused by other sampling gear (Holmes et al., 1990) or careless handling by field personnel. Apparently, even fresh hemorrhages that are relatively minor cannot always be attributed to electrofishing. Fredenberg (1992) found some lateral, intervertebral, and especially subvertebral hemorrhages in control fish. Likewise for Thompson et al. (1997a) who reported a rather high incidence of such injuries (16%) among brown trout controls captured in gill nets. Comparable evaluation of the incidence of spinal injuries and anomalies among "control" fish that are not electrofished is recommended to determine background levels of such occurrences and assist in the interpretation of injuries and anomalies found in electrofished specimens. For controlled experiments in which individual fish can be identified, biologists should consider pretreatment X-rays as suggested by McCrimmon and Bidgood (1965).

Even with X-rays, some vertebral damage, particularly hairline fractures, might go undetected or be hidden by potentially less severe injuries. Based on re-examination of 38 fish with X-rays 335 days after being electrofished and initially X-rayed, Dalbey et al. (1996) found that healing of spinal injuries resulted in significant calcification around and perhaps fusion of damaged vertebrae. Reclassification of these nearly year-old injuries based on the extent of healed tissues dramatically increased the proportion of severe, class-3 injuries over less severe class 1 and 2 injuries from 16 to 68% of all spinal injuries. They suggested that severity of injuries to vertebrae had been initially underestimated with many hairline fractures apparently overlooked or hidden by spinal compressions.

Relation Between Injury and Mortality

Taylor et al. (1957) concluded, based on limited evidence, that the primary cause of electrofishing mortality is physiological and only occasionally due to physical injuries. Many subsequent investigators, especially since the late 1980's, have reported high incidences of electrofishing-caused spinal injuries and associated hemorrhages in field operations or experiments but almost never mentioned the occurrence (or absence) of mortalities. Obviously, very severely injured fish would be expected to die. However, among the few papers specifically comparing incidences of immediate or short-term mortality and physical injury, none have reported an especially strong correlation between injuries and mortalities. Spencer (1967a), for example, reported that many bluegill killed by electricity in his experiments had no spinal injuries, whereas many of the survivors did. Based on another experiment with a small number of channel catfish, Spencer (1967a) concluded that many spinal injuries heal completely. After 45 days, even catfish with externally obvious spinal deformities survived and appeared to swim normally. Hudy (1985) similarly found that among trout with electrofishing-induced injuries, nearly 90% survived, although over half the injured survivors continued to exhibit abnormal swimming behavior or brands 15 days after the electrofishing event. Although McMichael (1993) reported only one death among over 120 hatchery rainbow trout exposed to DC and PDC fields and held for 7 days, he found that 25% of the treated fish had incurred vertebral injuries or hemorrhages, including 17% with broken backs. Habera et al. (1996) reported that 9% of 227 electrofished rainbow trout died within 7 days (13 of 20 mortalities were unrecovered fish assumed to be dead), but unlike a few survivors that were examined, none of the seven mortalities available for examination had incurred spinal injuries or associated hemorrhages. Fredenberg (1992) commonly observed old, healed spinal injuries in X-rays of trout collected in Montana—a further testament to the survivability of many fish with spinal injuries.

Factors Affecting Electrofishing Injury and Mortality

Electrical-field factors considered in the literature to affect the incidence of electrofishing-induced mortality and spinal injuries (including associated hemorrhages) include type of current, intensity, duration, orientation (relative to the fish), and for AC and PDC, waveform characteristics such as pulse or wave frequency, shape, and width. Related biological factors of concern include species, size, and condition.

Comparisons of results among and sometimes within publications and reports discussed in this section, as throughout the review, are difficult and often suspect because of differing or inadequately described biological, field, or experimental conditions, including electrical parameters. Even when electrical output and field intensity were reported for currents other than straight DC, authors frequently failed to indicate whether values represented peak or mean (rms in AC) measurements. Occasional mortalities have often been accepted as a normal consequence of electrofishing operations (and most other collection techniques) and as such may not be reported. Also, unless biologists specifically looked for and documented bruises or other external or behavioral signs of injury, absence of such information does not necessarily mean injuries did not occur. Even if externally obvious injuries were adequately documented, most internal injuries, as emphasized earlier, could only have been determined by X-ray analysis and necropsy. Despite

these limitations, the impact of some electrical and biological factors on electrofishing mortalities and injuries is reasonably clear, if not well understood.

Type of Current

Among types of current, most electrofishing authorities consider AC to be the most harmful to fish, DC the least fatiguing and injurious, and PDC somewhere between. Comparative field and laboratory investigations tend to support this generalization, but there are exceptions, and for each type of current, including AC, there are reports of no or insignificant mortality or injury (Appendix B). With sufficient field intensity and duration of exposure, any current can be lethal and, under certain conditions, even DC can injure substantial numbers of fish. The extent of mortality or injury caused by the different types of electrical currents (AC, DC, or PDC) varies considerably with how the currents are used (electrofishing techniques or procedures), electrical parameters (e.g., field size and intensity, pulse or cyclic frequency), biological factors (species, size, condition), and environmental conditions (e.g., water conductivity, temperature, basin configuration and dimensions).

Generally, immediate or short-term mortalities reported for PDC are as low or nearly as low as for DC (often none), but this does not appear to be the case with regard to spinal and associated injuries when using moderate to high-frequency PDCs. Although the incidence of such injuries detected for constant low-frequency PDCs (especially <20 Hz) and some specially designed PDC pulse trains (e.g., Coffelt's complex-pulse system, CPS) usually approaches or approximates the low levels observed for DC, that for constant moderate to high-frequency PDCs often approaches or approximates the substantially higher levels reported for AC. Because of the availability and commercial promotion of CPS as a less injurious form of PDC, it is treated in the literature and in this report as a distinct type of current, but its effects on fish might not be representative of other pulse-train configurations.

As discussed earlier under major responses of fish in electric fields, anodic taxis in PDC appears to differ from that in DC (Lamarque, 1990; Fredenberg, personal communication). Assuming the mechanisms involved and aspects of the current inducing taxis also differ, perhaps these differences are also responsible, at least in part, for the greater incidence of spinal injuries often observed under moderate to higher-frequency PDCs. Lamarque (1990) noted that injuries caused by DC occur mostly when fish lie motionless and tetanized near the cathode or when the current abruptly ceases or is reestablished. In the latter case (as when the current is repeatedly switched on and off), he suggested that DC momentarily acts like PDC.

Mortality. Amazingly little published data is available to support AC's reputation as the most lethal electrofishing current. Only investigations by Pratt (1955), Taylor et al. (1957), and DeMont (1971) compared incidences of mortality among fish subjected to AC with those similarly subjected to DC or constant-frequency PDC.

Taylor et al. (1957) conducted the only investigation comparing electrofishing mortality among all three types of current. In laboratory experiments (conductivity calculated as 1,494 μS/cm, but unusually high and uncertain; 16–18° C) with voltage gradients greater than required for narcosis, they exposed rainbow trout (20–23 cm) to homogeneous fields of 60-Hz AC (>0.3 V_p/cm), 12- to 20-Hz, triangular-wave PDCs (>1.5 V_p/cm at 12 Hz to >0.3 V_p/cm at 120 Hz with 33–88% duty cycles), and DC (>0.4 V/cm). Mortality was 4% for AC, just 0.3% overall for the PDCs and zero for DC. They also reported no mortality among larger (33-cm) and smaller (5-cm) rainbow trout similarly exposed to DC at field intensities greater than required for narcosis (>0.3 V/cm and >0.5 V/cm, respectively). Similar trends in mortality caused by these currents were observed when electrofishing in natural streams.

Pratt (1955) and DeMont (1971) also found fish more susceptible to mortality when exposed to AC than DC. In hatchery raceways (308 μS/cm), Pratt reported mortalities of 4% for rainbow trout ($\bar{x}$ = 19 cm), 10% for brook trout ($\bar{x}$ = 25 cm), and 20% for brown trout ($\bar{x}$ = 20 cm) electrofished with 110-V AC but only 2%, 0%, and 4%, respectively, with 230-V DC. In a series of electrocution experiments (200 μS/cm), DeMont (1971) found that substantially lower voltage gradients were required to kill 50% of threespine stickleback with AC (4.8 V/cm, probably rms) than with DC (14 V/cm); however, exposure times were twice as long for AC than for DC trials (20 s vs. 10 s), thereby confounding the comparison.

Unlike the preceding biologists, Spencer (1967b) found no consistent differences in lethal effects of 115-V AC and 115-V DC. In a series of concrete-pond experiments to assess the usefulness of electrofishing for killing intermediate-size (~8–10 cm) bluegill to thin populations, Spencer confined batches of test fish to a 0.3 by 0.9 m screened enclosure and, using the same electrodes, exposed them for 1 to 120 s to 230-V, 180-Hz AC (three phase); 115-V, 60-Hz AC (single phase); or 115-V DC (water resistivity reported as 6,000 ohms, which, if properly interpreted, calculates to a conductivity of 167 μS/cm). Survival was monitored for 24 h (prior experiments had revealed that only a very small percentage died after 24 h), and the number of dead fish was recorded at 5 min, 1 h, 2 h, 4 h, and 24 h. Percent mortalities generally increased with exposure time and, beyond 1 s, were always much greater for the 230-V AC (1–58%) than for either 115-V AC (0–19%) or 115-V DC (0–29%). For the 115-V

currents, percent mortality was sometimes greater for AC than DC and sometimes vice versa. Mortality was only substantially greater for AC than DC at 30-s exposures (3% vs. 0%) and 60-s exposures (9% vs. 4%), whereas it was substantially greater for DC than AC only at the 120-s exposure (29% vs. 19%). Interestingly, if the AC output is a mean (rms) rather than peak value, peak output and field intensity would have been about 41% greater than for DC. Trials for 230-V AC were extended with exposure times up to 300 s and resulted in up to 75% mortality. About 80% or more of the 230-V AC mortalities and 50% or more of the 115-V AC and DC mortalities occurred within the first 2 h after exposure. For exposures of 90 s or greater, over 90% of 230-V AC mortalities and over 50% of 115-V AC and DC mortalities occurred within the first hour (over 65% of 230-V AC mortalities for 90-s or longer exposures occurred within 5 min–no comparable data for other currents).

All remaining reports of AC mortality were non-comparative observations and, except for the report of 26% mortality by Hauck (1949, discussed earlier), none disclosed immediate or very short-term mortalities greater than 3%. Hudy (1985) observed less than 1% immediate mortality among 1,125 hatchery rainbow trout (16–26 cm) and 1,125 brook trout (12–24 cm) stunned with 250 to 300-Hz AC in a concrete raceway (350–760 V output; 10 μS/cm; 5.5° C) and reported that mortality increased to no more than 3% during the next 15 days. Schneider (1992) reported very little or no immediate or very short-term mortality (4 days) among yellow perch, bluegill, pumpkinseed, green sunfish, lake chubsucker, and golden shiner collected from Michigan lakes and ponds (66–520 μS/cm) using 3-phase AC. Output voltage was adjusted such that large fish recovered within 30 s but was high enough to stun small fish as well. Habera et al. (1996) reported 1% immediate and 3% 24-h mortality among rainbow trout (5–23 cm TL) electrofished with 60-Hz AC in a three-pass depletion population estimate (14 μS/cm; 15° C). No mortality was observed among control fish captured by angling.

Like Taylor et al. (1957), Edwards and Higgins (1973) and Dalbey et al. (1996, also Dalbey, 1994) compared DC and PDC and observed very little or no immediate mortality among exposed fish. In homogeneous field experiments to determine stun thresholds for channel catfish and bluegill in DC and 11 variations of PDC, Edwards and Higgins (1973) reported that the fish recovered instantly or within a few minutes and that very few deaths during the next 10 days could be traced directly to treatment in electric fields. Dalbey et al. (1996) similarly reported no immediate mortality for rainbow trout (15–39 cm FL) captured with DC, 60-Hz PDC, and a hybrid of the two.

Other investigators reported substantially greater mortalities for fish subjected to DC or PDC. Lamarque (1967a,b, 1990) reported immediate or very short-term mortalities of 6% and 17% for trout exposed for 20 s at a distance of 20 cm from the anode to two forms of DC (probably smooth and rippled) and 50 to 93% for those similarly exposed to four forms of constant-frequency PDC. However, peak field intensities were not reported and might have been substantially higher for the PDCs. Among rainbow trout (33–60 cm TL) and Colorado pikeminnow (30–39 cm TL) exposed to homogeneous 15- and 60-Hz, square-wave PDC, CPS, or DC for 5 s at various response threshold levels (530 μS/cm; 18° C), Meismer (1999) reported immediate mortality only among rainbow trout (10%) subjected to the highest intensity of 60-Hz PDC tested, 1 V_p/cm, a level sufficient to assure full tetany. In a separate laboratory comparison of effects on the same species by exposure to 10 s of 60-Hz, square-wave and 60-Hz, quarter-sine-wave PDCs (generated by Cofflet's VVP-15 and Smith-Root's GPP 5.0 electrofishers, respectively) at 1.5 V_p/cm, Meismer (1999) again reported immediate mortality only for rainbow trout (30%) exposed to the 60-Hz, square-wave current. Meyer and Miller (1990) reported no immediate mortality among rainbow and brown trout (29–54 cm TL) electrofished with 60-Hz PDC or CPS, but 3% delayed mortality (all within 2 days) among trout collected with 60-Hz PDC and held in a live net for 7 days. For rainbow trout (24–51 cm FL) collected during boat-electrofishing field trials (30 μS/cm; 7° C) to compare two currents at a time, Taube (1992) reported 5-day mortalities of 3% for DC versus 15% for 25-Hz PDC (75% duty cycle) for one set of trials but 11% for DC versus no mortality for CPS in another set of trials. In a non-comparative investigation using 450- to 650-V DC, Eloranta (1990) reported acute mortalities greater than 50% for burbot collected in the littoral zones of a lake (40–60 μS/cm) and less than 11% for most other species; mortality was greatest when operating at over 600 V.

Injury. Taube (1992) conducted the only published investigation comparing frequency of spinal injuries and associated inter-muscular hemorrhages among all three types of current. In controlled laboratory experiments (100–121 μS/cm, 9–13° C), he reported that incidence of spinal injury among large adult rainbow trout ($\bar{x}$ = 39–48 cm FL) was least for DC and CPS at 28 and 21%, respectively, intermediate for 60-Hz and two 30-Hz PDCs at 42–50%, and greatest for AC at 67%. Incidence of hemorrhages was also least for DC at 28% but similarly high, 42 to 46%, for all other currents. For each current, fish were exposed for 5 s in homogeneous fields at either of two levels of intensity, one just above the threshold for stun and the other much higher. However, differences in the number of injured fish at the two levels of intensity were not significant, and the data were combined for this comparison among current types. Most vertebral injuries were misalignments (class 2), and the remainder were spinal

compressions (class 1) with no detected vertebral fractures (class 3). Over half of the internal hemorrhages were severe (class 3).

Spencer (1967a) conducted the only other published comparison of AC and DC-caused incidences of spinal injury. He reported frequencies of injured bluegill as 0 to 3% for 115-V DC, 3 to 7% for 115-V AC, and 9 to 16% for 230-V AC. However, if reported AC voltage outputs were rms rather than peak, the comparison between 115-V currents is confounded by a 41% greater peak output voltage for AC.

In addition to Taube (1992), three other investigations have compared incidences of injuries caused by AC and PDC. McCrimmon and Bidgood (1965) reported no skeletal damage attributable to either current, Walker et al. (1994) reported substantially greater numbers of injuries for AC, and Hollender and Carline (1994) reported equally high frequencies of injuries for both currents.

McCrimmon and Bidgood (1965) exposed hatchery rainbow trout (11–27 cm TL) to either 60-Hz AC or 120-Hz, half-sine PDC (475–550 µS/cm, 11–13° C) and electrofished wild rainbow trout (6–59 cm TL) from Ontario streams with the same currents. All fish were X-rayed (the hatchery fish before and after exposure), and some were dissected. Among the hatchery fish, spinal anomalies were detected in 4% of the fish before exposure, but no new injuries were detected after exposure. Up to 16% of the wild fish, depending on the stream, had spinal compressions, but among a subsample also examined by necropsy, the compressed vertebrae were fused, immobile, and, therefore, not considered electrofishing injuries.

In a series of tests in aquaria (200–230 µS/cm; 12–14° C) to assess optimal currents, field intensities, and exposure times for narcosis without externally obvious injury, Walker et al. (1994) exposed juvenile northern pike (13–19 cm SL) to homogeneous fields of 50-Hz, sine-wave AC; 50-Hz, triangular-wave AC (0.4 to 2.1 V_{rms}/cm each); and 50-Hz PDC (36% duty cycle, 0.4–2.1 V_p/cm) for 10 to 60 s. Of the fish exposed to sine-wave AC, 24% remained on their sides for 16 to 24 h after exposure and had cutaneous hemorrhages (brands) along the entire body; some also had bent spines. They observed similar results for fish exposed to triangular-wave AC; 33% were injured and half of these remained on their sides throughout the 24-h observation period. However, with the triangular waveform, the hemorrhages occurred in the paired and median fins rather than along the body. In contrast to both AC currents, no externally obvious injuries resulted from exposure to 50-Hz PDC. More extensive tank-trials (410 µS/cm, 11° C) with adult northern pike (45–97 cm SL) subjected to 50-Hz PDC also resulted in no externally obvious injuries. No fish were X-rayed or necropsied.

Hollender and Carline (1994) electrofished brook trout (9–24 cm TL) in three small, low-conductivity streams (43–64 µS/cm, 8–11° C) and one moderate-conductivity stream (440 µS/cm, 11° C) in Pennsylvania with 250 to 300-Hz AC and 60-Hz PDC and subsequently examined them by X-ray and necropsy. Overall, they found hemorrhages or spinal damage in 26% (14–41%) of trout collected with AC and similar numbers, 22% (9–43%), among those collected with PDC. They also examined trout angled in those same streams as controls. They reported no hemorrhages or vertebral injuries among angled fish except in the moderate-conductivity stream where the incidence of vertebral damage, 12%, was comparable to the 14% observed for trout collected in the same stream with AC and 9% with PDC (least incidences of electrofishing injury among the four streams). Although the moderate-conductivity stream had been electrofished a year before, Hollender and Carline (1994) observed that most of the injuries in angled fish appeared to be more recent.

Among remaining reports of incidences of injury caused by exposure to AC fields, all of which are non-comparative, only Hauck (1949) and Spencer (1967a) reported substantial impacts. As discussed earlier (beginning of section on spinal and related injuries), Hauck (1949) described a variety of injuries that probably afflicted more than the 26% of rainbow trout that died within 2 to 5 days (Reynolds and Kolz in Reynolds et al., 1988). Spencer (1967a) observed spinal injuries in 6 of 10 channel catfish exposed to 230-V, 3-phase AC (presumably 180 Hz). The remaining investigators of AC impacts reported relatively few electrofishing injuries and suggested that, at least under similar circumstances, AC electrofishing is an acceptable technique for monitoring or assessing fish populations.

Among various coolwater and warmwater fish he electrofished with AC from various Michigan lakes and ponds (66–520 µS/cm, 0–28° C) and monitored for delayed mortality, Schneider (1992) reported externally obvious injuries only among yellow perch—50% had accumulations of bright-red blood in the sinus venosus near the base of the gills. The blood dispersed within a day, and all fish survived and appeared in good condition at the end of their respective holding periods (1–40 days). Schneider (1992) also emphasized that he rarely observed external indications of injuries among thousands of fish he had collected with AC, but he did not X-ray or dissect any of the fish.

In addition to a low incidence of mortality (1% immediate, 3% after 15 days), Hudy (1985) reported that after 15 days, less than 3% of 2,250 rainbow trout (16–26 cm) and brook trout (12–24 cm) electrofished in hatchery raceways (10 µS/cm, 6° C) with AC displayed externally visible physical or behavioral abnormalities (brands or erratic swimming). Based on X-rays, he detected an overall incidence of fractured or dislocated vertebrae in about 4% of the fish—21% of the mortalities, 77% of the abnormal

survivors, 1% of subsampled, normal-appearing survivors, and none of the control fish. Hudy (1985) observed that some fish in each treatment had fused vertebrae but assumed that these anomalies were not caused by electrofishing (he made no mention of compressed, unfused vertebrae).

Habera et al. (1996) assessed injury (and short-term mortality) among rainbow trout (5–23 cm TL) electrofished with 60-Hz AC in a three-pass depletion population estimate in a southern Appalachian stream (14 µS/cm, 15° C). No spinal injuries or hemorrhages were detected among mortalities (3%) or 12 angled controls examined by X-ray or necropsy, but among a subsample of survivors, 3% incurred class-2 spinal injuries and another 3% class-2 hemorrhages (6% combined). The injured fish were greater than 10 cm TL (12–17 cm) and collected only in second and third passes (fish taken during these passes may have been shocked but uncaptured in the preceding pass or passes). No external injuries (e.g., brands) or erratic swimming behavior were observed among survivors not X-rayed and necropsied.

Fredenberg (1992, personal communication), Taube (1992), and Meismer (1999) compared the injurious effects of DC with constant-frequency PDCs and the pulse train CPS in several investigations. Simple (constant-frequency) PDCs were usually more harmful than DC or CPS.

Comparing electrofishing injuries in rainbow trout (23–54 cm TL) collected from a wide range of Montana rivers and streams (33–900 µS/cm, 4–18° C), Fredenberg (1992) reported vertebral injuries in 5 to 18% of the trout collected with DC, 4 to 43% with CPS, and 13 to 68% (usually greater than 41%) for 60-Hz, square- and half-sine-wave PDCs. Incidences of inter-musculature hemorrhages were 0 to 25%, 25 to 77%, and 57 to 91%, respectively. Overall, spinal injuries or hemorrhages were found in up to 30% of the fish taken with DC and up to 98% of those collected with PDC (combined figures for CPS not reported). A hybrid of DC and 60-Hz PDC (Fig. 5J) resulted in spinal injury among 30% and hemorrhages among 72% of the collected rainbow trout. Many of the reported injuries in these collections were minor or class one.

In another investigation, Fredenberg (personal communication) also compared the incidence of spinal injuries, determined by necropsy, among adult ($\bar{x}$ = 38–42 cm TL) rainbow trout, mountain whitefish, and suckers (white and longnose) collected by three currents purported to be least damaging to fish: DC, 15-Hz PDC, and CPS. The fish were collected by boat electrofishing (cable electrodes) in late October from the Missouri River in Montana (450 µS/cm, 10° C). Despite a maximum (interpreted as peak) output voltage twice that for 15-Hz PDC and four times that for DC, he found CPS consistently least damaging. Among rainbow trout, CPS caused vertebral damage in just 2% and associated hemorrhages in 4% of the fish and DC just 6 and 2%, respectively. However, 15-Hz PDC caused spinal injuries in 20% and hemorrhages in 22% of the rainbow trout. Few, if any, injuries to the spine, just 0 to 2%, were observed for mountain whitefish or suckers regardless of the current. Incidences of hemorrhages (all minor, class 1) among mountain whitefish were again least for CPS and DC, just 2 and 6%, respectively, and greatest at 18% for 15-Hz PDC. In a reversal of the above results for DC and 15-Hz PDC, incidence of hemorrhages among suckers was greatest at 18% with DC, intermediate at 10% with 15-Hz PDC, and least at 4% with CPS.

Taube (1992) compared incidences of spinal injury among large rainbow trout ($\bar{x}$ = 38–42 mm FL) stunned in controlled experiments with heterogenous fields of DC, four variations of constant-frequency, square-wave PDC, and CPS. He found CPS to be significantly less harmful than the other currents, including DC. Output voltage was the same for all currents except CPS for which output was necessarily doubled to stun the fish. The trout were individually placed at the distal end of the exposure area in a raceway and chased towards the anode into an effective portion of the field where they were shocked (stunned) for 5 s. X-rays revealed spinal injuries in 8% of the fish subjected to CPS, 17% for DC, and 25 to 67% for various PDCs (20–60 Hz, 25–75% duty cycle). For comparable currents, these results were similar to those for his homogeneous-field experiments discussed above for comparison with AC. Most spinal injuries in both sets of experiments were recorded as misalignments (class 2) with some compressions only (class 1) and no fractures (class 3).

In one-on-one boat-electrofishing field trials in an Alaskan stream (30 µS/cm, 7° C), Taube (1992) also reported that rainbow trout ($\bar{x}$ = 32–40 mm FL) had spinal injury rates of 47% in DC versus 13% in CPS (difference not statistically significant), but on another day, 0% in DC versus 57% in 25-Hz PDC (75% duty cycle; difference statistically significant). He offered no explanation for the unusually high incidence of spinal injury in DC during the trial with CPS.

Combining treatments at various field intensity levels from the thresholds for twitch to 1 V_p/cm, which was sufficient to assure full tetany (n = 80 per species and current), Meismer (1999) found the percentage of Colorado pikeminnow (30–39 cm TL) with spinal injuries was significantly greater than controls (no injury) when exposed to 15-Hz, square-wave PDC (11%), but not DC (6%), CPS (6%), or 60-Hz, square-wave PDC (3%). For similarly treated rainbow trout (33–60 cm TL), the number of fish with spinal injuries was greater for exposures to CPS (5%) than DC (3%) or 15- or 60-Hz, square-wave PDC (each 1%), but differences between currents or relative to

controls were insignificant. All spinal injuries were minor (class 1) except for a slight misalignment in one Colorado pikeminnow exposed to DC. For Colorado pikeminnow, internal soft-tissue injuries, all minor (class 1) hemorrhages in or near the musculature of the spine, were detected in just a few specimens (1–3% for each current, none significantly different from controls). Hemorrhages were not assessed in the rainbow trout. Externally obvious injuries, all of which were brands (dark brown to black stripes or blotches, often in a zebra-like pattern), were common on rainbow trout regardless of treatment current, but significantly more so for those exposed to 60-Hz PDC (46% vs. 16–21% for the other currents). In stark contrast, Meismer (1999) observed no external injuries, brands or otherwise, on Colorado pikeminnow. For all treatment exposures (530 µS/cm; 18° C), field intensity was gradually increased to the desired response threshold or voltage gradient level and held there for 5 s.

If the muscular convulsions responsible for spinal injuries are induced by sudden changes in voltage, as suspected, then the spinal injuries documented in Meismer's (1999) experiments using DC must have occurred when the current was switched off at the end of exposure, or in the case of some rainbow trout observed by Meismer (1999), when they leaped frantically out of the water. Otherwise, it appears that such convulsions can occur as well, or instead, under constant current, as suggested by the observation of twitches in DC as the intensity was gradually increased to or beyond the threshold for that response. The question might be resolved by comparable experiments in which DC field intensity is also reduced gradually back to zero rather than suddenly switched off.

Fredenberg (1992), McMichael (1993), Dalbey et al. (1996), and Grisak (1966) compared frequency of injuries for fish subjected to DC and PDC exclusive of CPS. Fredenberg (1992), as in comparisons above with CPS, and Dalbey et al. (1996) also compared results for DC and 60-Hz PDC with results for a hybrid of the two currents (Fig. 5J). With one exception (Grisak, 1966), these investigators reported that DC caused far fewer injuries than 30 to 90-Hz PDC and that frequencies of injury for the hybrid current were intermediate but generally much closer to that for the PDCs.

Fredenberg (1992) necropsied and compared incidences of injury for brown trout (30–56 cm TL) electrofished with DC, 60-Hz PDC, and a hybrid of the two currents. Incidences of spinal injury and hemorrhages were 8 and 6%, respectively (10% combined), for brown trout electrofished with DC, 36 and 56%, respectively, for 60-Hz PDC, and 32 and 28%, respectively, for the hybrid current. However, in dramatic contrast to the frequency of injuries reported for brown trout, and earlier for rainbow trout, Arctic grayling (37–45 cm TL) examined by Fredenberg (1992) suffered no similar injuries when captured with DC and only a 4% incidence of hemorrhages when collected with the hybrid current (no data for 60-Hz PDC).

Based on X-rays, Dalbey et al. (1996, also Dalbey, 1994), like most other researchers, reported a substantially lower percentage of injured fish among wild rainbow trout (15–39 cm FL) captured with DC (12%) than with 60-Hz PDC (54%) or a hybrid of the two currents (40%). For all captures, they used the same mobile electrode system (Vincent, 1971) with a triangular anode thrown from a fiberglass boat and a peak output of 400 V (260 µs/cm, 13–16° C). Peak voltage gradients around the anode should have been identical regardless of the waveform used, but reported oscilloscope measurements were strangely much higher for DC than PDC or the hybrid current at least out to 1.2 m from the anode where reported values were about 4.7, 1.2 and 0.8 V_p/cm, respectively. At a distance of 2.4 m from the anode, measured peak voltage gradients were nearly the same, about 0.5 to 0.7 V_p/cm. Perhaps the DC voltage gradient at 1.2 m from the anode was measured perpendicular to a point of the triangle and the others perpendicular to the flat aspect of the anode between corners.

In a hatchery experiment, McMichael (1993) also found substantially fewer injuries among necropsied rainbow trout (14–48 cm FL) electrofished with DC than square-wave PDCs. For trout electrofished twice, 7 days apart, they reported 3% brands, 4% spinal injuries, and 4% hemorrhages among trout taken with DC at 300 V output, and 8, 14, and 17%, respectively, with DC at 400 V. In contrast, they reported 4, 22, and 35%, respectively, for trout taken with 30-Hz PDC at 300 V and 58, 35, and 53%, respectively, with 90-Hz PDC at 300 V output. However, if output voltages for the PDCs were mean rather than peak values, their reported duty cycles of 12.5% (McMichael, personal communication) would have resulted peak output voltages of 2,400 V and the PDC fields would have been six to eight times more intense than the DC fields, thereby confounding comparison between types of current.

Grisak (1996) studied the effects of electrofishing on four non-salmonid fishes in the Missouri River, Montana. Unlike many other investigators, he reported that when data were combined for all species X-rayed and necropsied, more spinal injuries were caused by DC than 40-Hz PDC (25% duty cycle), 14% and 5% respectively, and the same frequency of muscular hemorrhages, 14% (about half class 1 and half class 2) for each current (only 3% of the injured fish had both spinal damage and hemorrhages). However, this generalization is misleading. Among the four species reported upon, only goldeye (11–37 cm TL), the predominate species captured, was injured using DC and for this species the incidence of

spinal injury was far greater for DC than 40-Hz PDC, 21% and 4%, respectively. In contrast, incidences of hemorrhages among goldeye were considerably fewer for DC than PDC, 21% and 39%, respectively, and percentages with either spinal injuries or hemorrhages, or both, were also less for DC than PDC, 32% and 43%, respectively. Grisak (1996) suggested that goldeye's usually high incidence of spinal injury when captured with DC might have been associated with its especially strong taxic response to DC or resultant proximity to or contact with the anode. Among the other three species collected and examined, all reported injuries were caused by 40-Hz PDC: flathead chub (8% spinal; 11–24 cm TL), shorthead redhorse (5% hemorrhage; 18–49 cm TL), and river carpsucker (18% spinal, 9% hemorrhage, 27% combined; 30–58 cm TL). All fish succumbed to tetany but revived within minutes of capture and no brands were observed with either current. Among control fish collected by other means, Grisak (1996) reported only one fresh internal injury, a spinal compression.

Several investigators compared frequencies of injury among fishes captured or exposed to simple (constant-frequency) PDCs with those for fish captured or exposed to CPS. As in most above comparisons of CPS with DC and PDC, Meyer and Miller (1990), Sharber et al. (1994) and Ruppert and Muth (1997) found CPS less harmful than 30-Hz or greater PDC, but Meyer and Miller (unpublished manuscript, 1991) reported similar spinal injury rates for brown trout taken by the two currents and higher percentages for rainbow trout taken with CPS than 40-Hz PDC.

Based on X-rays of single-pass, field-collected fish from the Laramie River (600–610 μS/cm) in late April and early May 1990, Meyer and Miller (1990) reported that 78% of rainbow trout (30–36 cm TL) and 82% of brown trout (28–54 cm TL) taken with 60-Hz PDC incurred spinal injuries, whereas, 50% of the rainbow trout (30–41 cm TL) and 25% of the brown trout (13–59 cm TL) were similarly injured when taken with CPS. Sample sizes were small, but during the previous September in the Wind River (299 μS/cm; September), comparable injury rates (60% for rainbow trout, 26–43 cm TL, and 86% for brown trout, 17–51 cm TL) were also observed for 60-Hz PDC among a much larger number of previously uncaptured trout taken during the fourth pass of a population estimate effort. However, some of those injuries might have occurred during earlier passes and the electrofishing control box was seriously out of calibration (output voltage and actual PDC characteristics questionable) and might have been partially responsible for the high incidence of spinal injuries (CPS was not used in the latter effort).

In September 1990, Meyer and Miller (unpublished manuscript, 1991; Wyoming Fish and Game Department, 1991) repeated the comparison of current-induced spinal injuries but used 40-Hz rather than 60-Hz PDC and collected the fish from the Wind River (340–350 μS/cm; 7–8° C). The frequency of spinal injuries was much lower than the prior spring in the Laramie River and, with one exception, was similar for both 40-Hz PDC and CPS. Spinal injuries were observed among none of the X-rayed rainbow trout (16–31 cm TL) and 15% of the brown trout (17–41 cm TL) taken with 40-Hz PDC as compared with 12% and 14% of the fish, respectively (both species 16–39 cm TL), taken with CPS. On the same day, during the fourth pass of a population estimate, captures of trout not previously captured using 40-Hz PDC in a downstream segment of the same river also revealed far fewer injuries (35% for rainbow trout, 14–40 cm TL, and 26% for brown trout, 17–38 cm TL) than during the prior year, but injuries were notably greater than for upstream single-pass captures. Some of the fourth-pass injuries probably occurred earlier in September during the first three passes for that population estimate.

Sharber et al. (1994) compared the frequency of spinal injuries revealed by X-rays of adult rainbow trout (>30 cm TL) captured with 15-, 30-, 60-, and 512-Hz, square-wave PDC and CPS at night in the Colorado River below Glen Canyon Dam (600–800 μS/cm, 9–11° C). They found that for PDC injury rates increased with pulse frequency from 3 to 24, 43, and 62%, respectively, and that the percentage of injured fish for CPS, 8% (range 7–9%), was less than for 30-Hz, but not 15-Hz PDC. Although 15-Hz PDC generated fewer injuries than CPS, it is presumably less effective for attracting and capturing fish (Sharber, personal communication).

Ruppert (1996) and Ruppert and Muth (1997) compared the frequency of vertebral injuries and muscular hemorrhages near the spine in juvenile bonytail (5–8 cm TL) exposed in laboratory experiments (940 μ, 15° C) to 10 s of homogeneous CPS and 30-, 60-, and 80-Hz, square-wave PDC at predetermined voltage-gradient thresholds for taxis, narcosis, and tetany. No vertebral damage was detected, but spinal hemorrhages, all class 2 with an average of three per fish, were observed in 13% of all treatment fish (range of 3–27% for individual treatments, none in controls). Combining field-intensity treatments, mean frequency of hemorrhages was least for CPS, 8%, and ranged from 10 to 19% for the constant-frequency PDCs. Among juvenile humpback chub (5–10 cm TL), similarly subjected to CPS, no spinal injuries were detected but 20% had muscular hemorrhages (insufficient specimens for comparable trials with PDCs).

As noted above, McCrimmon and Bidgood (1965) reported no spinal injuries among hatchery or wild rainbow trout exposed to 120-Hz, half-sine, PDC. Fredenberg (1992) also reported no spinal injuries or hemorrhages among walleye and sauger collected with 60-Hz PDC. Similarly, Dwyer and White (1995) reported no spinal trauma among

hatchery rainbow trout (about 33 cm TL), including four mortalities, individually exposed to 10 s of homogeneous 250-Hz, half-sine PDC at 3.5 to 3.9 V_p/cm (0.9–1.0 V_m/cm; 270–340 µS/cm, 8° C). Mitton and McDonald (1994a) exposed rainbow trout (30–600 g) in tanks to 20 to 40 s of 60-Hz PDC with output voltages of 200 to 600 V (240–270 µS/cm, 7 and 15–20° C), and detected spinal injuries with X-rays only in a few of the largest fish. They concluded that PDC electrofishing does not normally produce any skeletal damage. These reports of no injury using constant-frequency PDC are in stark contrast to an ever-increasing number of field studies in which substantial numbers of fish were injured when subjected to PDC.

Many of the comparative studies noted above revealed substantial incidences of spinal injuries and hemorrhages for fish captured with or exposed to constant-frequency PDC. Among investigations comparing or reporting on only PDCs, Sharber and Carothers (1988, 1990), based on X-rays and necropsy, reported spinal and associated soft-tissue injuries in 44 to 67% of 209 large rainbow trout (30–56 cm TL) that were boat (raft) electrofished at night in the Colorado River below Lake Powell (450–600 µS/cm, 10–11° C) in two successive years using 60-Hz, square, quarter-sine, and exponential PDCs. Spinal injuries were not observed in 12 nonelectrofished hatchery trout of similar size. Reynolds and Kolz (in Reynolds et al., 1988) calculated approximate voltage gradients of about 8.6 V_p/cm at the surface of the spherical anode, 0.5 V_p/cm at 0.5 m, and about 0.15 V_p/cm at 1 m from the anode.

Reynolds and Kolz (in Reynolds et al., 1988) reported that recent studies by the Alaska Department of Fish and Game corroborated Sharber and Carothers' (1988) findings. In a Kenai River investigation (50 µS/cm at 7° C), 11 of 22 large rainbow trout (>40 cm FL) suffered spinal injuries. The Alaskan investigators noted that injuries seemed more likely among trout captured within 0.5 m of the anode where voltage gradients were greater than 1 V/cm.

In addition to the experiments discussed above, Meismer (1999) observed brands on most rainbow trout exposed for 10 s in homogeneous, 1.5 V_p/cm fields of 60-Hz, square-wave and 60-Hz, quarter-sine-wave PDCs (95% and 50%, respectively). However, the incidence of spinal injuries was insignificant (15% and 5%, respectively). In contrast, no external or internal injuries were detected in Colorado pikeminnow similarly exposed to either PDC.

Field Intensity

It is well documented that beyond threshold levels, the lethality of electrofishing fields generally increases with field intensity (i.e., voltage gradient, current density, or power density). However, as with other responses to field intensity, the lethal physiological effects of field intensity appear to be a function of the voltage differential it causes across the fish and that differential also depends on the orientation of the fish relative to the lines of current.

Unlike mortality, the relation between electrofishing-induced injuries and field intensity, beyond some threshold level, remains unclear. Like severe stress, fatigue, and mortality, spinal and related injuries have long been attributed to intense, tetany-causing currents, especially in AC fields. But contrary to this long-held belief, such injuries are not restricted to the higher intensities required for tetany or even narcosis. Spinal injuries, and the myoclonic jerks assumed to be their principal cause, might not even be possible while a fish is in a state of narcosis (petit mal) or full tetany (grand mal). Recent studies clearly document that spinal injuries are just as likely to occur at or above the threshold for twitch in the zone of perception as in more intense portions of the field, regardless of the type of current. Accordingly, and unlike severe stress, fatigue, and mortality due primarily to apnea (respiratory failure) and muscular tension (tetany), measures to reduce the intense zone of tetany around an electrode might not have much impact on the frequency of spinal injuries. As discussed below, there is evidence both for and against increasing incidences, and perhaps severity, of spinal injuries as field intensity increases beyond the threshold for injury. Since the threshold for seizures sometimes causing spinal injuries (threshold for twitch), occurs in the zone of perception, the number of fish sustaining spinal injuries and escaping the field and capture might be significant, perhaps as great as among the fish that are caught.

Mortality. The effect of field intensity on mortality was dramatically demonstrated by Lamarque (1967a,b, 1990). Trout (probably brown trout) were exposed for 20 s at distances of 20 cm and 50 cm from the anode using a variety of DC and PDC currents. At 20 cm, where field intensities were much higher, mortalities resulted with all six currents tested (6–93%, Appendix B), but at 50 cm, mortalities were observed for only one of these currents (90 Hz, half-sine PDC) and for that current were far fewer than at 20 cm (27% vs. 89%).

However, the importance of electrical-field intensity as a cause of fish mortality was documented much earlier by other researchers. For homogeneous 60-Hz AC fields (39 µS/cm based on a reported water resistivity of 10,000 ohm/in^3 (interpreted as ohm-in); 12° C), McMillan (1929) documented the increase in mortality with increased field intensity for YOY (young-of-the-year) chinook salmon ($\bar{x}$ = 7.9 cm FL). For fish exposed for 1 min, mortality rose from none at 0.5 to 0.6 V_m/cm (<threshold for stun) to 10% at 0.7 V_m/cm, 39% at 0.8 V_m/cm, and 57% at 1.0 V_m/cm. For fish exposed for 5 min, mortality rose from none at 0.2 to

0.5 V_m/cm to 62 to 69% at 0.6 to 0.7 V_m/cm and 67 to 79% at 0.8 V_m/cm.

In brief summary of the responses of sardines and topsmelt to DC and a variety of PDCs in sea water (>50,000 μS/cm), Groody et al. (1950) noted that current densities greater than 5.4 mA/cm^2 "seemed to have a detrimental effect on the fish in the form of temporary paralysis or death, depending on duration of the current and the size of the fish" and that this was especially true for non-pulsating current (DC). As discussed earlier under "Comparison of Currents for Electrofishing Purposes," Groody et al. (1950) concluded that among tested currents, 3- to 4-Hz, square-wave PDCs with duty cycles of 67 to 75% were not only most effective in producing taxis but least injurious (interpreted as least lethal). Unfortunately, the details of their experiments and results were apparently not published.

Using very-low-frequency, square-wave PDC (2-Hz, 20-ms pulses) in fresh water, Collins et al. (1954) reported that mortality for four size-groups of (YOY) chinook salmon (4–12 cm TL) increased in direct proportion to increases in voltage gradient (and current density) from a threshold at 3.5 to 4 V_p/cm to 57 to 78% at 15 V_p/cm (48 μS/cm, 10–20° C). In these homogeneous-field experiments, fish were held parallel to the lines of current for 30 s. In a similar set of experiments but with voltage gradient held constant at 4 V/cm and water conductivity increased incrementally from 50 to 500 μS/cm (thereby increasing current density), they found that mortality generally increased with current density from a threshold level (first incidence) at a current density between 0.17 and 0.41 mA/cm^2 to 8 to 75% at 1.9 mA/cm^2, but results varied greatly within and among groups and temperature ranges (10–19.9° C and 20–25° C).

In a set of heterogenous 15- and 30-Hz, 8.3-ms, square- and half-sine-wave PDC experiments in a raceway (15–17° C) with YOY coho salmon (6–10 cm SL) forced through sequentially activated electrode arrays, Pugh (1962) reported mixed results but generally greater mortality in the more intense electric fields. Trials were run with peak output voltages of 165 or 250 V at water conductivities of 67, 100, 200, and 1,000 μS/cm. Overall, short-term (24-h) mortality ranged from 1 to 18% ($\bar{x}$ = 8%) at 250 V versus 1 to 8% ($\bar{x}$ = 5%) at 165 V. Immediate mortality among controls ranged from 2 to 4%. With output held constant at 250 V and data averaged for the two lower conductivity levels, mortality increased with increasing current density (increased conductivity). However, no similarly consistent differences were observed when output was held at 165 V. Test and control fish were held for 30 days to assess delayed mortality; although mortality ranged from 2 to 29% and 5 to 15%, respectively, no significant differences were detected (5% level).

As described under "Type of Current," Spencer (1967b) compared the lethal effects of 230-V AC to 115-V AC on bluegill (8–10 cm) exposed for 1 to 120 s. He reported far greater 24-h mortalities for 230-V AC than for 115-V AC, up to 58% and 19%, respectively. However, the two currents differed in more than intensity—the 230-V AC was a three-phase, 180-Hz current, whereas the 115-V AC was a single-phase, 60-Hz current. Spencer (1967b) also exposed bluegill to 60 s of the 230-V AC in another set of experiments for which water conductivity was increased in several steps from 100 to 1,000 μS/cm (thereby also increasing current and power density; water conductivities calculated from reported water resistivities of 10,000 to 1,000 ohms [interpreted as ohm-cm]). In these experiments, 24-h mortality increased progressively with water conductivity and field intensity from 4 to 56%.

In one set of data for which Whaley (1975) subjected bluegill and fantail to 45 s of 9-Hz PDC (154 μS/cm, 10° C), mortality increased progressively from about 21 to 44% and 19 to 37%, respectively, as voltage gradient increased from 3.1 to 5.0 V/cm. In another set of data, also incorporating exposures 30, 60, 120, and 180 s (apparently a different set of experiments since 45-s exposure did not correspond to the aforementioned), a similar pattern of progressively increased mortality with voltage gradient for both species was apparent only for exposures greater than 45 s. Especially for exposures beyond 45 s, the effect of voltage gradient on mortality increased with duration of exposure. For exposures of 180 s at 5 V/cm, mortality was about 95% for bluegill and 100% for fantail darter. Whaley (1975) observed no indication of an interaction between the effect of field intensity and fish length.

Much more recently and contrary to the above research, Hudy (1985) reported very low mortalities (0.5–1.8%) with no statistically significant differences among voltage levels (350-V, 700-V, and 760-V output) for 2,250 hatchery rainbow trout (16–26 cm) and brook trout (12–24 cm) subjected to very high-frequency AC (250–300 Hz; 10 μS/cm, 6° C). However, Sharber (in Sharber and Hudy, 1986) suggested that very low water conductivity and the type of electrodes used (radio antennae and 25- and 50-cm hoops) probably resulted in relatively small, low-current-density fields (except very close to the electrodes) and that few mortalities would be expected in such weak fields. Low water temperature (6° C) might also have minimized mortality.

Among rainbow trout (33–60 cm TL) and Colorado pikeminnow (30–39 cm TL) exposed to homogeneous 15- and 60-Hz, square-wave PDC, CPS, or DC gradually increasing to and held for 5 s at threshold levels for twitch, taxis, or narcosis, or 1 V_p/cm to assure full tetany (530 μS/cm; 18° C), Meismer (1999) reported immediate mortality (10%) only at the highest intensity level and then only

for rainbow trout subjected to 60-Hz PDC. In a separate experiment under the same conditions, Meismer (1999) reported still higher immediate mortality, 30%, for rainbow trout exposed directly (rather than gradually) to the same current at an even higher intensity level of 1.5 V_p/cm for 10 s.

As with other responses to a specific field intensity, the orientation of fish in an electric field is a critical factor in determining whether the field is strong enough to cause mortality. Collins et al. (1954) demonstrated its importance in a homogeneous-field experiment with 7-cm fish held either parallel or perpendicular to the lines of current at 6 V/cm. Fish held parallel to the lines of current experienced 42 V along their bodies (fish length x voltage gradient) and suffered 77% mortality, whereas fish held perpendicular to the field experienced only about 6 V across the body (about 1 cm in width) and all survived. Exploratory experiments revealed no differences in mortality whether fish faced the anode or the cathode. Collins et al. (1954) concluded from these experiments that the effective, mortality-producing factor in field intensity is the total voltage differential across the fish (head-to-tail voltage, or side-to-side voltage if perpendicular to the lines of current).

Whaley et al. (1978; also Whaley, 1975) tested the survival of bluegill (9–17 cm) and fantail darter (3–8 cm) held parallel to the lines of current in homogeneous PDC fields (up to 16 Hz) and reported as much as 75 to 95% mortality when exposed for 2 or 3 min at 4 V/cm (154 μS/cm, 10° C). Recognizing that their test fish were always subjected to the maximum voltage differential available, they suggested that under natural conditions in a stream, the percentage of fish killed directly by electrofishing should be notably less because fish would be randomly located in a heterogenous field, primarily aligned with water current, and therefore, subjected to varying head-to-tail voltages.

Various factors other than orientation were reported to compound the effect of field intensity on mortality. Nearly all biologists testing the factor found that mortality at a particular field intensity (above the threshold) increased with time of exposure (McMillan, 1929; Collins et al., 1954; Spencer, 1967b; Whaley, 1975; Whaley et al., 1978). When voltage gradient was held constant, mortality also generally increased with water temperature (Collins et al., 1954) and, in PDC, with pulse frequency (Collins et al., 1954; Whaley, 1975; Whaley et al., 1978).

In an experiment with disconcerting results, Zeigenfuss (1995) subjected several hundred 15- to 35-cm-TL hatchery-reared rainbow trout to homogeneous fields of 60-Hz, square-wave PDC for 2 s at 1.6 V/cm (probably peak) in spring of one year (283 μS/cm, 10–12° C) and 3.2 V/cm the next spring (226 μS/cm, 8° C). Contrary to expectations, immediate and short-term mortality (within 24-h) was greater at the lower field intensity (9%) than the higher field intensity (2%), but short-term mortality among measured and tagged controls was not reported for comparison. Zeigenfuss (1995) suggested that warmer water temperatures were probably responsible for the substantially higher immediate and short-term mortality during the first-year trial. He observed that mortality varied throughout the day but was lowest among those shocked in the morning and increased among those shocked in the afternoon (presumably as water temperature increased). During the second-year trial, water temperatures remained low and mortality was low and constant. There was no apparent relationship between incidences of mortality and incidences of spinal injury. Although injured fish had a higher incidence of mortality than shocked uninjured fish, the difference was not significant. Also, there was no correlation between length and mortality of shocked fish.

Injury. Experiments by Spencer (1967a), Roach (1992), and Mitton and McDonald (1994a) suggest that the incidence of spinal injuries increases with field intensity. In controlled pond experiments, Spencer (1967a) consistently found two to three times more spinal injuries in bluegill subjected to more intense AC fields—9 to 16% at 230 V and 3.1 A versus 3 to 7% at 115 V and 2.0 A. However, two different forms of AC were used, a three-phase, 180-Hz current for the former and a single-phase, 60-Hz current for the latter. Similarly, Roach (1992) observed greater incidences of vertebral injuries among adult northern pike (38–74 cm FL) exposed for 5 s to homogeneous fields of 30 or 60-Hz PDC (50% duty cycles) at 400 V_p than at 100 V_p output (109–132 μS/cm; 11–16° C). For 30-Hz PDC, incidence of spinal injury was 10% at an output of 400 V_p (measured voltage gradient of 0.98 V_m/cm) versus 5% at an output of 100 V_p (0.25 V_m/cm). For 60-Hz, incidence of spinal injury was 12% at 400 V_p (1.76 V_m/cm) versus 8% at 100 V_p (0.44 V_m/cm). (Note that voltage gradients reported by Roach, 1992, are inconsistent with current or output parameters—assuming the same wave shape, same output voltage, and a constant distance between electrodes, PDCs with the same duty cycle should produce the same mean or peak voltage gradients, regardless of frequency; with square-waves, a 50% duty cycle, and plate electrodes positioned at the ends of the 91-cm-long exposure tank, mean field intensity should have been about 2.2 V_m/cm for output of 400 V_p and 0.56 V_m/cm for a peak output of 100 V_p). Mitton and McDonald (1994a) exposed 65 rainbow trout in 50-, 100-, and 600-g size groups each to 20 or 40 s of 60-Hz PDC (5-ms) with outputs of 200, 400, or 600 V (240–270 μS/cm; 7° C). Of all fish tested, only two of the

15 largest (600-g) specimens (13%) exposed at the highest field intensity (600 V output) experienced spinal injuries, both class 2 involving three vertebrae.

In contrast to the above observations, several investigators have reported no significant relationship between incidence of injury and field intensity. Taube (1992), using equipment similar to that used by Roach (1992), exposed large adult rainbow trout ($\bar{x}$ = 39–48 cm FL) for 5 s to low-intensity (100 V output, at or above threshold level for stun) and high-intensity (400-V output) homogeneous fields of AC, DC, 30-Hz and 60-Hz PDC, and CPS (100–121 µS/cm; 9–13° C). But unlike Roach (1992), Taube (1992) found no significant differences in the frequency of spinal injury or hemorrhages attributable to differences in tested field intensities for any current (incidences of injury ranged from 17 to 75% depending on the type of current). [Taube, 1992, did not indicate whether reported output voltages for PDC and CPS were peak or mean values, nor how he measured voltage gradients, but there were considerable discrepancies between measured values (e.g., for DC, about 0.5 V/cm for 100 V output and 0.9 V/cm for 400 V output) and what might have been expected based on output voltage divided by maximum distance between electrodes (e.g., about 1.1 V/cm and 4.4 V/cm, respectively). However, if voltage gradient was measured while each fish occupied the tank, their considerable length and volume relative to the exposure tank probably affected voltage gradient throughout much of the tank. Voltage gradients for currents other than DC were reported as mean values.] For northern pike (also the subject of Roach's 1992 experiments), Walker et al. (1994), found no correlation between incidence of externally obvious injury (including failure to swim upright within 16 to 24 h of exposure) and treatment field intensities between 0.4 to 2.1 V_{rms}/cm for either sine-wave or triangular-wave 50-Hz AC, regardless of exposure time (10, 30, or 60 s; 200–230 µS/cm, 12–14° C). Nor did they report any such injuries for a comparable series of experiments using 50-Hz PDC. However, Walker et al. (1994) did not X-ray or necropsy fish for detection of internal injuries. Hudy (1985) reported low percentages of spinal-injury (0.8–2.4%) for hatchery rainbow trout and brook trout exposed to 250 to 300-Hz AC, but with no significant differences among tested output voltages (350-V, 700-V, and 760-V). As noted above for mortality, Sharber (in Sharber and Hudy, 1986) suggested that Hudy's (1985) fish might not have been subjected to the high field intensities implied by his output voltages. However, field intensities were obviously high enough to induce at least narcosis. Just as confounding is the report of no injury by McCrimmon and Bidgood (1965) for hatchery-reared rainbow trout (11–27 cm). McCrimmon and Bidgood (1965) exposed their trout two to four times for 3 to 10 s each in 60-Hz AC fields averaging 0.8 and 1.5 V/cm and 120-Hz, half-sine PDC fields averaging 0.7 and 1.4 V/cm. In this case, water conductivities and temperatures were moderate (475–550 µS/cm, 11–13° C), and at least the higher voltage gradients should have been sufficient to induce tetany, although such was not specifically mentioned.

Like his results for immediate and short-term mortality (discussed above), Zeigenfuss (1995) reported a substantially greater incidence of spinal injury among fish subjected to the lower of two field intensities. Based on lateral-view X-rays, he detected a 70% incidence of spinal injuries for rainbow trout exposed to 2 s of 60-Hz, square-wave PDC at a homogeneous 1.6 V/cm, but only 40% for those similarly exposed to a field with twice the field intensity (3.2 V/cm). However, nearly all that difference was accounted for in the least-severe class of spinal injuries (class 1, compressions); in both high and low-intensity fields, only 4 or 5% of the fish incurred class-2 injuries and no more than 2% incurred class-3 injuries. No injuries were detected among control fish. Upon necropsy, Zeigenfuss (1995) found minor hemorrhaging in subsamples of both control and shocked fish. These were mostly thin spikes extending from between vertebrae into the muscle and suspected to be artifacts of freezing because many were not associated with obvious vertebral damage. The only fish with severe, class-3, hemorrhages were shocked fish with class-2 spinal injuries from the lower-intensity treatment. Among fish from the higher-intensity trials, all presumably electrofishing-induced hemorrhages were class 1 and none were aligned with vertebral injuries.

In laboratory experiments, Meismer (1999) clearly proved that at least minor (class 1) spinal injuries are just as likely to occur at the threshold for twitch near the outermost margins of the perceived electric field as within the effective portion of that field (zones of taxis, narcosis, and tetany). Meismer (1999) exposed rainbow trout (33–60 cm TL) and Colorado pikeminnow (30–39 cm TL) to homogeneous fields of various currents (15- or 60-Hz, square-wave PDC, CPS, or DC; 530 µS/cm, 18° C) by gradually increasing field intensity from zero to the observed threshold for twitch, taxis, or narcosis or 1 V_p/cm (sufficient to assure full tetany), then holding the fish at that treatment level for 5 s. Combining data for the different currents, the percentages of rainbow trout with spinal injuries were 4% for twitch, 1% for taxis, 1% for narcosis, and 4% for tetany. For Colorado pikeminnow, they were 11, 4, 5, and 6%, respectively. Of both species, only the number of Colorado pikeminnow exposed up to and at the threshold for twitch (11%) was significantly greater than for controls (no injuries). All spinal injuries

were minor except for a slight misalignment (class 2) in one Colorado pikeminnow exposed in DC at the threshold for narcosis. Although exposures at each higher response level included ramping intensity through all lower thresholds, the data do not suggest cumulative increases in spinal injuries (all or most injuries could have occurred at the lowest threshold). Incidences of detected hemorrhages at or near the spine were few and insignificant for Colorado pikeminnow (1%, 0, 3%, and 3%, respectively); hemorrhages were not assessed for rainbow trout. In contrast to spinal injuries, the incidence of brands significantly increased with treatment field intensity from 4% for twitch, to 19% for taxis, 34% for narcosis, and 46% for tetany. This trend was evident for all treatment currents except DC.

In another set of experiments, Meismer (1999) exposed both species directly to a still higher field intensity of 1.5 V_p/cm in either of two waveforms of 60-Hz PDC (square and quarter-sine) for 10 s and reported an even higher incidence of branding (73%) for rainbow trout than discussed in the preceding paragraph. Although the overall incidence of spinal injury for rainbow trout in this experiment was 10%, it was not significantly different from the control or incidences of injuries for lower intensity treatments in Meismer's (1999) previously discussed experiments. Like the previously discussed experiments, no brands were observed on Colorado pikeminnow, but unlike those lower intensity treatments, neither were spinal injuries or associated hemorrhages. Again, hemorrhages were not able to be assessed for the trout.

For most other investigations comparing frequency of spinal injuries for fish subjected to different levels of field intensity, results were mixed or inconclusive. For example, Sharber et al. (1994) conducted field experiments in the Colorado River (600–800 µS/cm, 9–11° C) and concluded that differences in field intensity near the anodes had no significant effect on the percentage of large rainbow trout with X-ray-detected spinal injuries. However, the results in that regard should probably be considered inconclusive. Electric fields were generated by 12 A_p of 60-Hz, 4-ms, square-wave PDC between a spherical 30-cm cathode and one of three different types and sizes of anodes. The anode assumed to have the lowest near-field intensity (that near the surface of the anode), a 1-m Wisconsin ring with ten 20-cm droppers, required an output of 215 V_p, and resulted in injuries to 43% of the large trout collected. A 30-cm sphere anode was assumed to represent an intermediate near-field intensity, required 315 V_p, and also resulted in injuries to 43% of the fish. A 1.2-m-long by 1-cm-diameter steel cable was assumed to represent a high near-field intensity, required 380 V_p, and resulted in injury to 65% of the fish. Despite capture and examination of fewer fish using the cable electrode (23 vs. 60 for the dropper ring and 116 for the sphere), the latter result suggests that high-intensity fields near an electrode can cause substantially more injuries. However, because fish appeared to be attracted to the lower end of the cable electrode and were stunned farther below the water surface than with the other electrodes, Sharber et al. (1994) noted that the fish were more difficult to net and suggested that the higher incidence of trout injuries for the cable electrode might have been due to longer exposure time rather than the higher intensity of the field near the electrode's surface.

The electrical resistance of an electrode (or electrode array) and field intensity next to its surface are inversely proportional to its exposed surface area, whereas the shape and distribution of field intensity beyond the surface but within a few multiples of the principal dimension depend on the shape, size, and orientation of the anode. Reynolds and Kolz (1995) calculated the surface areas of the anodes used by Sharber et al. (1994) and suggested that the sphere rather than the Wisconsin ring in their investigation had the least resistance and least intense electric field near its surface, but their calculations assumed a smooth surface for the cable anode and the droppers of the Wisconsin-ring anode. The rough, convoluted surface of stranded or braided cable that was probably used has a considerably greater surface area. Also, the output voltages required to maintain a current of 12 A_p between the anode and cathode support Sharber et al.'s (1994) assumption that anode resistance and near-electrode-surface field intensity was least for the Wisconsin ring and greatest for the cable. Even so, because most fish were probably captured some distance from the anodes and because Sharber et al. (1994) failed to document the magnitude and distribution field intensity around each anode with actual voltage-gradient measurements, relative field intensity somewhat beyond anode surfaces and that to which the fish were actually exposed remains uncertain (Reynolds and Kolz, 1995; Sharber et al., 1995).

Regardless of the limitations and interpretation of the above experiment, Sharber et al. (1994) reported that in this and a related experiment, as well as experiments reported by Sharber and Carothers (1988), few if any captured specimens exhibited symptoms of tetany despite high incidences of injury. Based on this remark, anecdotal observations, and circumstantial evidence, such as brands on fish netted relatively far from the electrodes, field intensities high enough to induce tetany are not required to cause spinal injuries and such injuries can occur anywhere within at least the effective portion of the field, and possibly outside the threshold for taxis (Sharber and Carothers, 1988; Sharber and Carothers, in Reynolds et al., 1988; Meyer and Miller, 1991, unpublished manuscript, 1991; Sharber et al., 1994). Lamarque (1990) noted that a single pulse and sometimes a low voltage

can be sufficient to cause the violent contractions resulting in such injuries (but he did not elaborate) and Meismer (1999), as discussed above, proved in homogeneous field experiments that spinal injuries are just as likely to occur at the threshold for twitch as in more intense portions of the field.

As in the comparison of anode systems by Sharber et al. (1994) above, Thompson (1995) and Thompson et al. (1997a) compared the injurious effects of two anode systems with significantly different near-field intensity and reported mixed results. However, in this case, the authors actually measured peak field intensity for each event at 15 cm from the anodes—2.3 to 7.4 V/cm for the single throwable anode of a boat electrofishing system and 0.5 to 1.2 V/cm for the multiple anode array (four or five hand-held anodes) of a shore-based wading system. Using 60-Hz, half-sine-wave PDC, approximately 50 rainbow trout (13–51 cm TL) and 50 brown trout (10–49 cm TL) were collected, frozen, and later X-rayed and necropsied for each electrofishing system from each of three Colorado rivers (90–270 µS/cm, 1–7° C). Incidences of spinal injury and associated hemorrhages in rainbow trout were greater for the higher-intensity throwable anode system (18–64% spinal injury and 28– 65% hemorrhage, 32–76% combined) than the multiple anode wading system (6–40% spinal injury and 13–49% hemorrhage, 13–58% combined). For brown trout (10–49 cm TL) incidences of hemorrhages were also greater for the throwable anode than the multiple anode system (24–45% and 13–30%, respectively) but incidences of spinal injuries were similar for both high and low-intensity anodes (18–52% and 27–38%, respectively). Combined incidences of spinal injury and hemorrhage for brown trout were 36–61% and 25–51%, respectively. In addition to considerable overlap in incidences of injury between the higher and lower near-field-intensity systems, rank for incidence of injury within each system usually, but not always, correlated with rank for corresponding near-field intensity for rainbow trout but not for brown trout. Brown trout often incurred the least incidences of spinal injuries in the most intense fields. Despite relatively high rates of internal injury, Thompson et al. (1997a) noted that very few of the fish exhibited external signs of injury. Spinal injuries were not only most numerous but also most severe for rainbow trout collected with the more-intense, throwable-anode system (10–27% for class 1, 8–30% for class 2, and 0–13% for class 3). For rainbow trout collected with the less-intense, multiple-anode, wading system and brown trout collected with by either system, most spinal injuries were class 1 (6–32%), half as many were class 2 (0–20%) and very few were class 3 (0–2%). Control rainbow trout and brown trout, which were collected by angling or gill net from river segments not recently electrofished and by dip net from rearing raceways, had 7–11% spinal injuries (one class 2 and the rest class 1). Among control fish collected by angling and dip net, only one hemorrhage (a class 3 wound) was detected, but among controls taken by gill net (all rainbow trout), 16% had hemorrhages (one class 3 wound and the rest class 1).

Ruppert (1996) and Ruppert and Muth (1997) compared the frequency of vertebral injuries and muscular hemorrhages near the spine in juvenile bonytail (5–8 cm TL) exposed to 10 s of homogeneous CPS and 30-, 60-, and 80-Hz, square-wave PDC (2.6-, 4-, 4-, and 5-ms pulses) at field intensities corresponding to predetermined thresholds for taxis (0.8 V_p/cm for CPS and 0.4–0.5 V_p/cm for the others), narcosis (1.0 and 0.6–0.7 V_p/cm, respectively), and tetany (1.4 and 1.0–1.1 V_p/cm, respectively; water 950 µS/cm and 15° C). The anticipated responses were achieved in all treatment fish. Based on low-power microscopic examination of the spines in filleted fish, no vertebral damage was detected for any treatment fish or controls, but spinal hemorrhages, all class 2 with an average of three per fish, were observed in 13% of all treatment fish (range of 3–27% for individual treatments, none in controls). Combining electrical-current treatments, frequency of spinal hemorrhages was greatest for tetany-level treatments (18%), least for narcosis (11%), and intermediate for taxis (13%). However, rank for frequency of hemorrhages among response intensity levels varied with individual treatment currents. The highest mean incidence of hemorrhages occurred at the taxis level for 80-Hz PDC (23%), the narcosis level for CPS (10%), and tetany level for 30- and 60-Hz PDC (20 and 27%, respectively). Although higher field intensities tend to induce a higher frequency of spinal hemorrhages, this obviously is not always the case. Sometimes, as many or more injuries can occur in fish subjected to field intensities no higher than those needed to induce taxis (perhaps even lower).

Voltage differentials across fish must exceed some minimum value (threshold) before muscular seizures and spinal injuries are likely to occur. Thus, orientation of fish when first exposed to the effective portion of the field (or later) is probably as significant a factor as it is for other responses and mortality. However, in preliminary laboratory experiments, Sharber (personal communication) found the situation for spinal injuries to be opposite that discussed above for mortality (Collins et al., 1954). Using 60-Hz, 4-ms, square-wave PDC to produce a homogeneous field, he recorded injuries in over 30% of trout held perpendicular to the electric current (head-to-tail voltage least) but in only 3% of trout held parallel to the current (greatest heat-to-tail voltage differential). For trout held perpendicular to the current, reduction of pulse frequency to 15-Hz (5-ms) also reduced injuries to 3%. These results further indicate that high

field intensities and head-to-tail voltage differentials might not be critical factors in electrofishing injuries, at least when using PDC. The results also correlate well with early observations by Haskell et al. (1954) that upon circuit closure, muscular bending of fish toward the anode was greatest when fish were oriented perpendicular to the current and almost nil when they were oriented parallel to the current. The matter deserves confirmation and further investigation. Evidence that spinal-related injuries are usually far fewer in DC than PDC (see discussion under "Type of Current") indicates that some attributes of PDC fields in addition to field intensity must be responsible.

Duration of Exposure

Concentration (in this case, field intensity—discussed above) and duration of exposure are the most critical factors in determining the effects of most chemicals and physical parameters on the physiology, behavior, and survival of organisms. So it is with the lethal and sublethal stressful effects of electric fields. Increased mortality with increased exposure time has been well documented, especially at field intensities sufficient to induce tetany. But beyond a necessary minimum threshold, and although addressed in only a couple investigations, duration of exposure in AC and DC fields does not appear to have an important effect on spinal and related injuries. However, this might not be the case for PDC (or pulsed AC). Observations of a direct relation between pulse frequency and injuries (discussed later) suggest that duration of exposure also should be important because longer exposures would subject fish to more pulses.

As noted above under "Field Intensity," McMillan (1929) and Collins et al. (1954) reported increases in mortality of YOY chinook salmon with increases in duration of exposure. Using 60-Hz AC, McMillan documented mortality rates of 10 to 57% for 1 min exposures at 0.7 to 1.0 V_m/cm versus 62 to 79% for 5 min exposures at 0.6 to 0.8 V_m/cm. Using 2-Hz, square-wave PDC (20-ms pulses, 4% duty cycle), Collins et al. (1954) held treatment fish ($\bar{x}$ = 7 cm TL) parallel to the lines of current at three homogeneous levels of field intensity (water about 50 μS/cm, 10 to 20° C). At 1 V/cm, a 15-min exposure resulted in 2% mortality and a 20-min exposure in 17% mortality. At 2 V/cm, the exposure threshold for mortality was 5 min when 6% of the fish succumbed; longer exposures of 7.5, 10, and 15 min resulted in 12, 32, and 30% mortality, respectively. At 4 V/cm, mortality increased progressively with exposure time from 1% for 0.5 min to 52% for 10 min; it then dropped to 39% and 48% for 11- and 12-min trials and rose again to 77% for 13 min, the longest exposure tested. In another experiment with voltage gradient held constant at 2 V/cm in 50 μS/cm water (100 μA/cm^2), Collins et al. (1954) reported that mortality increased progressively from 2 to 4% for 3- to 3.5-min exposures to 59% for a 10-min exposure. With water conductivity increased to 85 μS/cm (0.17 μA/cm^2), exposure times of 2, 3, 4, 5, 7.5, and 10 min resulted in 4, 6, 44, 37, 58, and 48% mortality, respectively. They further reported that the effect of duration of exposure on mortality in PDC increased directly with size of fish, water temperature, and pulse frequency but not pulse duration.

Like Collins et al. (1954), Whaley et al. (1978; also Whaley, 1975) also found that mortality increased with duration of exposure for PDC. Based on tests of fantail darter (3–8 cm) and bluegill (9–17 cm) held parallel to the lines of current in a homogeneous field at 4 V/cm (154 μS/cm, 10° C), they reported that mortality was low to negligible for exposures up to 15 s and that thereafter recovery time and mortality increased progressively with longer exposures. Mortality was greater than 35% for 2-min exposures and greater than 50% for 3-min exposures. The effect of exposure time was compounded by increases in pulse rate such that greatest mortalities (75–95%) were recorded for the longest exposures (2 and 3 min) at the highest pulse rate tested (16 Hz). Of the two factors, they concluded that exposure time had the greater impact on mortality. Referencing unpublished data by O. Maughan and C. Schreck, Whaley et al. (1978) noted that mortality also increased with exposure time for fathead minnow and bluegill subjected to electric fields for up to 4.5 min (160 V output; form of current and field intensity not noted).

As discussed under "Type of Current," Spencer (1967b) conducted a series of experiments to assess the usefulness of electrofishing for killing intermediate-size (~8–10 cm) bluegill to thin populations. In doing so, he subjected confined batches of test bluegill to 1 to 120 s of 230-V AC, 115-V AC, and 115-V DC (heterogenous fields in a concrete pond) and monitored survival for 24 h. In each case, mortality increased progressively with exposure time (with a few minor deviations)—from 1 to 58% for 230-V AC, 0 to 19% for 115-V AC, and 0 to 29% for 115-V DC. Trials for 230-V AC were extended up to 300 s and mortality continued to increase to 75%. About 80% or more of all 230-V-AC mortalities and 50% or more of mortalities for the other currents occurred within 2 h after exposure. For exposures of at least 90 s, over 90% of 230-V-AC mortalities occurred within the first hour and over 65% within the first 5 min after exposure. Over 50% of mortalities for the other currents occurred within the first hour (no 5-min data).

Although Spencer (1967b) and others discussed above found time of exposure to be a critical factor in electrofishing mortality, Spencer (1967a) found no significant relation between duration of exposure and incidence of spinal injury for bluegill exposed to the same currents and range of exposure times. Accordingly, he

concluded that these injuries occur immediately when fish are first exposed to the electric field.

Walker et al. (1994) also reported no correlation between injury and exposure time (10, 30, or 60 s), although they observed externally obvious injury (or failure to swim upright within 16–24 h) among 24% and 33% of juvenile northern pike subjected to 50-Hz, sine- and triangular-wave ACs, respectively. As noted under "Type of Current," they observed no such injuries in a comparable series of experiments using 50-Hz PDC. However, no fish in these experiments were X-rayed or necropsied for internal injuries not reflected in external damage or abnormal swimming behavior. No additional reports were found on the effect of exposure time on incidences of spinal or related injuries.

Exposure times utilized in these and other experiments on the effects of electric fields on fish vary from a second to several minutes or longer. In electrofishing practice, 20 s is a long exposure; in rivers, most fish are subjected to electrofishing fields for less than 10 to 15 s (Bestgen, personal communication). However, fish may be subjected to much longer exposures when they encounter electrical barriers or guiding devices or when electricity is used, like a chemical anesthetic, to induce narcosis for handling or experimental purposes (see earlier discussion under "Zones of Narcosis and Tetany"). For example, using DC at a homogeneous intensity level just sufficient to maintain narcosis with fish still actively breathing (0.25 V/cm, 13–21° C, 450 μS/cm), Kynard and Lonsdale (1975) exposed yearling rainbow trout (~12 cm) for 1,2, 4, or 6 h but reported mortalities (7%) only for the 6-h trials. Recovery to normal swimming and feeding was almost instantaneous for fish exposed up to 2 h but required up to half a day for some fish exposed for 6 h.

Waveform, Pulse Shape

The effect of waveform or pulse shape on AC or PDC-electrofishing mortality or injury has been poorly studied and remains inconclusive. Exponential, and half-sine (rectified AC) PDC and square-wave PDC, in separate studies, have been implicated as particularly lethal and quarter-sine PDC and square and half-sine PDCs, again in separate studies, as particularly injurious. A comparison of sine-wave and triangular-wave AC revealed no significant differences in incidence of externally obvious injuries in exposed fish but notable differences in the nature and perhaps severity of those injuries.

Vibert (1967b), in agreement with Halsband (1967), claimed that exponential (i.e., capacitor or condenser-discharge) waveforms have the greatest physiological effect on fish and are therefore among the best waveforms for electrofishing. But according to his associate, Lamarque (1967a), use of exponential waveforms in electrofishing was based on the false assumption that best results always are obtained with high voltage or tetanizing currents. Lamarque (1967a) observed that exponential waveforms can kill an eel in 30 s and concluded that with their steep initial slopes and short pulse durations exponential waveforms are the worst form of PDC. Lamarque (1967a,b, 1990) further documented the adverse effects of exponential, as well as half-sine, waveforms in tests conducted with an assortment of gear in a stream. For trout exposed to electric fields for 20 s while being held about 20 cm from and facing a 40-cm ring anode, he reported mortalities of 86 to 93% when using 80-Hz, exponential waveforms (33% and 50% duty-cycle) and 89% when using a 90-Hz, 400-V, half-sine waveform (rectified AC, probably full-wave because no duty cycle was reported). For other waveforms, mortalities were substantially less—50% mortality for a 5-Hz, 400-V, 33% duty-cycle, square waveform; 17% for a 400-V, rippled DC (partially smoothed, rectified AC); and only 6% for 500-V DC. Testing fish in the same currents at 50 cm from the anode, he recorded mortalities for only the half-sine PDC waveform (27%). Lamarque (1967a) suggested that the high mortalities for the exponential and sine-wave PDCs tested might be attributed to their high frequencies. If output voltage was mean rather than peak, the more lethal currents were also more intense than the DC currents, and as discussed earlier, intensity is a very important factor in electrofishing mortality.

In a one-on-one laboratory comparison, Meismer (1999) found 60-Hz, square-wave PDC generated by Cofflet's VVP-15 electrofisher was much more lethal to adult rainbow trout (30% immediate mortality) than 60-Hz, quarter-sine-wave PDC generated by Smith-Root's GPP 5.0 electrofisher (no immediate mortality). The fish were exposed at 1.5 V_p/cm for 10 s (530 μS/cm; 18° C). Large subadult Colorado pikeminnow were similarly tested but experienced no immediate mortality.

Although Lamarque (1967a,b, 1990) concluded that exponential and half-sine waveforms were among the most lethal of PDC waveforms, Sharber and Carothers (1988, 1990), did not report any immediate mortalities for large rainbow trout (30–56 cm TL) collected from the Colorado River using similar waveforms. However, they did find that 60-Hz, quarter-sine PDC was more injurious than either 60-Hz, exponential or square-wave PDCs—67% of the fish had X-ray-detected spinal injuries versus 44% and 44%, respectively. Both the quarter-sine and square waveforms had a 25% duty cycle (4-ms pulses) and were output at 260 V_p. Quarter-sine-wave PDC also damaged significantly more vertebrae per fish ($\bar{x}$ = 9.5) than exponential PDC ($\bar{x}$ = 6.6), but the number of vertebrae damaged by square-wave PDC ($\bar{x}$ = 8.2) was not statistically different from either. Spinal injuries were not observed in 12 nonelectrofished trout of similar size from a hatchery.

In a similar comparison of electrofishing injuries, Fredenberg (1992) reported very high injury rates for rainbow trout and brown trout collected from several drainages in Montana using both 60-Hz, square-wave (~8-ms pulses) and half-sine-wave (both half and fully rectified AC, ~8- and ~16-ms pulses) PDCs—78 to 98% and 62 to 90% of the fish, respectively. Fewer fish were injured using square-wave CPS (pulse train; 15-Hz packets or bursts of three 240-Hz pulses) or a hybrid DC-PDC waveform (top half of 60-Hz, half-sine pulses over a half-voltage DC baseline)—31 to 54% and 44 to 64%, respectively. These percentages are based on combined data for X-rays and necropsy (Sharber and Carothers 1988 and 1990 considered only vertebral damage based on X-rays) and do not take into account substantial differences in severity of the injuries. The data include minor hemorrhages likely to have been discounted or overlooked by others (Fredenberg, personal communication).

In addition to the differences in mortality discussed above for a one-on-one laboratory comparison, Meismer (1999) found 60-Hz, square-wave PDC somewhat more harmful than 60-Hz, quarter-sine-wave PDC for adult rainbow trout. When exposed for 10 s to the square-wave PDC at $1.5 V_p$/cm, 95% of the trout suffered brands, but when similarly exposed to the quarter-sine PDC, only 50% suffered brands. Meismer (1999) also reported that 15% of the rainbow trout exposed to the square-wave current and 5% of those exposed to the quarter-sine current experienced minor spinal injuries, but neither incidence of injury was significantly different from controls (no injury). Large subadult Colorado pikeminnow were similarly tested with both waveforms, but experienced no detectable external or internal injuries.

The typical waveform for AC currents is a sine wave, but others are possible. Walker et al. (1994) compared the narcotic and externally obvious injurious effects of 50-Hz, sine- and triangular-wave ACs, at various field intensities and exposure times in juvenile northern pike. Differences in the incidence of injuries between these currents were unpredictable, but there were relatively consistent differences in the nature and severity of those injuries. Fish injured when exposed to sine-wave AC (24% of the fish) had cutaneous hemorrhages (brands) along their entire body length and all failed to swim upright within 16 to 24 h, whereas those injured when exposed to triangular-wave AC (33% of the fish) had hemorrhages in their paired and median fins, and half of those (17%) failed to recover upright swimming within 16 to 24 h.

Pulse Frequency

Pulse frequency appears to be a primary factor affecting PDC-caused spinal injuries and may be a significant, but probably secondary, factor in electrofishing mortalities. If, as strongly suspected, most spinal injuries and related hemorrhages in electric fields are caused by sudden changes in electrical potential, as when currents are switched on and off, then it should not be surprising that investigators have generally reported increasing incidences of such injuries with increasing PDC frequency. Only a couple of studies suggested no relationship. If field intensity and exposure time are maintained above the threshold for lethal effects, there is some evidence that mortality can also be greater when using higher-frequency PDCs.

As mentioned in the preceding section (Waveform, Pulse Shape), Lamarque (1967a) suggested that high mortalities observed after 20-s exposures near the anode using exponential and half-sine PDCs (86–93%) might have been caused by the high pulse frequencies of those currents, 80 and 90 Hz, respectively. But even for 5-Hz, square-wave PDC, he reported 50% mortality. With regard to injuries in PDCs, Lamarque (1990) suggested that extent of injury depends mainly on pulse frequency and pulse duration. He concluded that "the worst currents are those with a pulse duration of 2–5 ms at 5–200 Hz." Yet these are precisely the PDC ranges most used in recent decades, including currents designed to reduce the occurrence of spinal injuries.

Collins et al. (1954) and Whaley et al. (1978; also Whaley, 1975) provided two of only three other reports of the effects of PDC pulse frequency on electrical-field mortality. In both cases, pulse frequencies were limited to no more than 16 Hz. Collins et al. (1954) reported that mortality among YOY chinook salmon exposed for 30 s to homogeneous fields of square-wave PDC increased with pulse frequency from none for 5-cm fish at 3 Hz to a maximum of 75% for 11-cm fish at 15 Hz (4 V/cm, 768 μW/cm^3, 20-ms pulses, 48 μS/cm). Whaley et al. (1978; also Whaley, 1975) found that mortality of fantail darter and bluegill exposed for 60 to 180 s in homogeneous PDC also increased with pulse rate (and exposure)—from 20 to 69% at 2 Hz and 32 to 77% at 9 Hz to 62 to 95% at 16 Hz (4 V/cm, 154 μS/cm, 10° C). Noting that Northrop (1967) had reported poor taxis for frequencies of 10 Hz or less, Whaley et al. (1978) concluded that their "... data showed relatively high mortality of fantail darters and bluegills in the pulse frequency defined as giving good electrotactic response." Collins et al. (1954) reported that mortality rates were compounded by both increased exposure times and increased size. Whaley et al. (1978) also reported that mortality was compounded by exposure time but did not observe a size-of-fish effect. Noting that pulse duration, and therefore the total energy applied per unit time, did not appear to influence the incidence of mortality, Collins et al. (1954) concluded that "change in potential" and the

rate at which such occurs (i.e., pulse frequency, switching current on and off) significantly affected the extent of electrofishing mortality.

In a comparison of the harmful effects of 15- and 60-Hz, square-wave PDC on fish (530 μS/cm; 18° C), Meismer (1999) reported that, after gradually increasing homogeneous field intensity to beyond the threshold for full tetany and holding it for 5 s at 1 V_p/cm, rainbow trout experienced an immediate, but insignificant, mortality of 10% in the 60-Hz current, but none in the 15-Hz current. All trout survived similar treatments in these currents at lower field intensities (thresholds for twitch, taxis and narcosis). Meismer (1999) similarly tested subadult Colorado pikeminnow with these PDCs and both species with CPS and DC but observed no other cases of immediate mortality.

Combining data for the various field intensities in these same experiments, Meismer (1999) found that although rainbow trout suffered insignificantly few spinal injuries in any current, they were much more susceptible to brands when exposed to 60-Hz PDC (46%) than 15-Hz PDC (16%), or either of the other two currents tested (19–21%). In contrast and contrary to general expectations, he found Colorado pikeminnow, which suffered no brands in any treatment, more susceptible to spinal injury when exposed to 15-Hz PDC (11%) than 60-Hz PDC (5%) or the other currents tested (6% each). However, all spinal injuries but one were minor (class 1) and only the percentage of fish with spinal injuries exposed to the 15-Hz PDC was significantly different from controls (no injury).

Northrop (1962, 1967) reported that all brown trout (20–25 cm) he subjected to 33- and 100-Hz, square-wave PDCs (20- and 5-ms pulses, respectively) recovered within a few minutes, swam, and reacted normally to external stimuli, but that those subjected to the 100-Hz current were immediately narcotized (tetanized), precluding the taxis observed at 33-Hz, and had bloody vents. He attributed this internal bleeding to violent uncoordinated muscle spasms caused by the higher-frequency current. Unlike Northrop (1962, 1967), most subsequent investigations of electrofishing injuries relative to PDC frequency were based on X-ray analysis or necropsy.

McMichael (1993) and McMichael and Olson (unpublished manuscript 1991—exclusive source of brand data) reported substantially higher incidences of brands, vertebral damage, and associated hemorrhages among hatchery-reared rainbow trout (14–48 cm FL) exposed twice to 90-Hz, square-wave PDC (58%, 35%, and 53%, respectively) than those similarly exposed to 30-Hz, square-wave PDC (4%, 22%, and 35%, respectively). No injuries were detected among unexposed controls. Electric fields were produced in separate raceway pens using a backpack electrofisher with an output of 300 V and duty cycle of 12.5% (McMichael, personal communication). After initial exposure, the fish were processed (anesthetized, measured, weighed, scale samples removed, and tagged) and monitored for 7 days. Following the 7-day monitoring period, they were recaptured with the same currents, iced, and necropsied within 2 h.

Field experiments in the Colorado River by Sharber et al. (1994) also support a direct relation between spinal injuries to large rainbow trout and pulse frequency for square-wave PDCs (600–800 μS/cm, 9–11° C; spherical electrodes). Based on X-rays alone, they reported spinal injuries among 3% of the fish taken at 15 Hz, 24% at 30 Hz, 43% at 60 Hz, and 62% at 512 Hz (pulse width was 4-ms at all frequencies except 512 Hz, where it was 0.2-ms). A laboratory test in homogeneous 15-Hz PDC at 0.5 V/cm also resulted in injury to 3% of the fish (Sharber, personal communication).

Although Taube (1992) also documented very high incidences of spinal injuries and related hemorrhages for large rainbow trout exposed to homogeneous square-wave PDCs, and his data suggest a tendency for more injuries at higher frequencies, he reported no significant difference in injury rates between currents of 30 Hz (33–58% spinal injuries, same for hemorrhages) and 60-Hz (42–58% spinal injuries, 33–50% for hemorrhages). Likewise, for trout exposed to heterogeneous fields of 20-Hz (25–58%), 30-Hz (33%), and 60-Hz, square-wave PDC (67%).

Contrary to the above reports of high incidences of spinal injury to rainbow trout subjected to moderate and high-frequency PDCs, McCrimmon and Bidgood (1965) and Dwyer and White (1995), as discussed earlier under "Type of Current," reported no electrically induced spinal injuries for rainbow trout (11–27 cm and ~33 cm, respectively) exposed to 120- and 250-Hz, half-sine PDC, respectively. Also as discussed in that earlier section, Mitton and McDonald (1994a) detected very few spinal injuries among rainbow trout (~600 g) they exposed to 60-Hz PDC for 20 to 30 s. However, these were non-comparative investigations with respect to PDC frequencies.

Although much less obvious and serious than injuries usually observed in trout (Roach, personal communication), Roach (1992) observed a higher percentage of vertebral injury in northern pike (36–74 cm FL) exposed to homogeneous fields of 120-Hz PDC (28%) than 30- and 60-Hz PDCs—28% versus 5–12%. However, the results are confounded by field intensities, water conductivities, and water temperatures that also differed (300–600 V, 0.93 V_m/cm, 1,017–1,090 μS/cm, 10–13° C for the 120-Hz PDC vs. 100 or 400 V_p, 109–32 μS/cm, 0.25–1.76 V/cm, 11–16° C for the 30 and 60-Hz PDCs). Over an output range of 50 to 300 V, Roach (1992) also observed spinal-related hemorrhages among 15% of pike exposed to 60-Hz PDC but none among those exposed to 30-Hz PDC.

Remaining investigations for non-salmonids failed to demonstrate a significant relationship between pulse frequency and spinal injuries or hemorrhages. Newman (1992; unpublished manuscript, 1991) reported spinal injuries for 25% of walleye (18–48 cm TL) collected in lakes using 120-Hz PDC and 31% for those collected in rivers using 30-Hz PDC. However, output voltage (mean or peak not specified) was 200 V at 120 Hz versus 310 V at 30 Hz and water temperatures were also warmer for the 30-Hz collections (26° C vs. 22° C). For juvenile bonytail (5–8 cm TL) exposed to 10 s of homogeneous 30-, 60-, and 80-Hz, square-wave PDC (4-, 4-, and 5-ms pulses) at voltage-gradient thresholds for taxis, narcosis, and tetany (940 μS/cm, 15° C), Ruppert (1996) and Ruppert and Muth (1997) observed no vertebral damage via low-power microscopic examination but reported a non-significant tendency for increased incidences of spinal hemorrhages with increased pulse frequency. Combining field-intensity treatments, frequency of spinal hemorrhages (all class 2 with an average of three per fish) averaged 10% (3–20%) at 30-Hz, 14% (7–27%) at 60-Hz, and 19% (13–23%) at 80-Hz. However, the differences were not significant and the overall tendency for hemorrhages did not hold for taxis and tetany-intensity treatments. At the intensity level required for taxis, incidence of hemorrhages was the same for 30- and 60-Hz PDCs (7%) and at the tetany level, incidence of hemorrhages was the same for 30- and 80-Hz PDCs (20%) and greatest for 60-Hz PDC (27%).

Perhaps, as suggested by Collins et al. (1954) for mortality, convulsions resulting in spinal injury occur predominantly as the current or pulse is "switched on." This might explain why fewer spinal injuries generally occur at lower frequencies in PDC and perhaps why even in straight DC (no pulses) some spinal injury has been observed (DC momentarily acting like PDC when switched on and off—Lamarque, 1990). Indeed, Haskell et al. (1954) documented that in sufficiently strong fields, fish responded to each circuit closure with a muscular seizure that resulted in a bending of the body towards the anode. Interestingly, and counter to the concept of greater head-to-tail voltages yielding stronger responses, Haskell et al. (1954) found that the more nearly perpendicular the fish was to the lines of current, the stronger the bending response. Fish in line with the current exhibited little, if any, bending of the body. Perhaps the convulsions resulting in these bends occur on both sides of the body but are proportionally stronger on the side facing the anode and essentially equal when the fish is parallel to the current.

Pulse Trains

Pulse trains are a complex variation of PDC frequency usually consisting of a short series of higher-frequency pulses (referred as trains, packets, or bursts) delivered at a lower secondary frequency. For example, Coffelt Manufacturing's CPS (complex pulse system) consists of trains of three very rapid 240-Hz, 2.6-ms pulses delivered at a secondary frequency of 15 Hz (resulting in a 12% duty cycle). Most PDCs are simple and characterized by constant pulse frequency, intensity, shape, and width, but many pulse trains and other complex variations are possible and some have become commercially available—CPS and Smith-Root's P.O.W. (programmable output waveforms including custom pulse trains) and "sweeping" PDC waveforms (pulse frequency or width gradually reduced to a specified level over a 10-s interval). However, of these, only the CPS pulse train has been included in reported investigations of lethal or injurious effects. Whether other pulse trains or sweeping waveforms are more, less, or comparably injurious to fish remains to be documented.

Only two very limited investigations compared the immediate or short-term lethal effect of CPS with one or more other currents. For large rainbow trout electrofished in a one-on-one comparison from an Alaskan stream, Taube (1992) reported no deaths for CPS and 11% mortality for DC. However, as discussed above under "Type of Current," Taube (1992) also reported only 3% mortality for DC versus 15% for 25-Hz PDC in another one-on-one comparison on another day. Also for adult rainbow trout, as well as large subadult Colorado pikeminnow, Meismer (1999) compared the adverse effects of CPS with those of DC and 15- and 60-Hz, square-wave PDC at various field intensities from the threshold for twitch to a level sufficient to assure tetany, 1 V_p/cm. He reported no immediate mortalities for any CPS or other treatment except rainbow trout exposed to the 60-Hz PDC at the highest intensity level (10% mortality, but not significantly different from controls which suffered no mortality).

In general, CPS has been found to be as effective as low-frequency PDCs, and sometimes DC, for minimizing spinal injuries. However, as for low-frequency PDCs (<20 Hz), some, but not all, biologists have found the current less effective for taxis and capture of fish than higher-frequency PDCs (see earlier discussion on "Comparison of Currents for Electrofishing Purposes").

Meyer and Miller (1990, 1991, unpublished manuscript, 1991; Wyoming Game and Fish Department, 1990, 1991) reported CPS to be less injurious than 60-Hz, square-wave PDC but, depending on species, comparable to or even in more injurious than 40-Hz, square-wave PDC. Among fish collected and X-rayed from the Laramie River in spring 1990 using 60-Hz PDC, they reported that 78% of the rainbow trout (30–36 cm TL) and 82% of the brown trout (28–54 cm TL) had incurred spinal injuries, whereas, 50% of the rainbow trout (30–41 cm TL) and 25% of the brown trout (13–59 cm TL) collected with CPS were similarly injured. Among fish collected from the Wind River

the following fall with 40-Hz PDC, none of the X-rayed rainbow trout (16–31 cm TL) and 15% of the brown trout (17–41 cm TL) incurred spinal injuries whereas with CPS, 12% and 14% of the fish, respectively (both species 16–39 cm TL), were injured. Output voltages were about 20 to 25% higher for CPS (460–470 V) than 40-Hz PDC (370–390 V) to maintain comparable sampling efficiency.

Fredenberg (1992) compared injuries among trout electrofished with CPS and other currents in Montana. Combining damage to the spine with associated hemorrhages (including minor ones that may have been discounted or overlooked by others—Fredenberg, personal communication), he reported that CPS caused notably fewer injuries (31 to 54% of captured fish) than 60-Hz, square-wave or half-sine-wave PDCs (62 to 98%), and somewhat fewer injuries than a hybrid DC-PDC waveform (Fig. 5J; 44 to 64%), but more injuries than DC (7 to 30%).

In another investigation, Fredenberg (personal communication) compared incidences of injury for selected species (white and longnose sucker, rainbow trout, and mountain whitefish) collected in the Missouri River (October 1990, 10° C, about 450 μS/cm) using CPS and other currents often recommended to minimize electrofishing injuries. He reported fewer total injuries using CPS (400 V, 22.4 A) than DC (110 V, 5 A) and 15-Hz PDC (200 V, 17.5 A)—2 to 6% (0–2% for vertebral damage only) versus 8 to 18% (0–6% vertebrae only) for DC and 10 to 42% (2–20% vertebrae only) for 15-Hz PDC.

For large rainbow trout exposed to homogeneous or heterogeneous fields under laboratory or hatchery conditions, or heterogeneous fields in an Alaskan stream, Taube (1992) also found incidences of spinal injuries caused by CPS to be lowest among tested currents. In homogeneous trials, Taube (1992) reported spinal-injury frequencies of 17 to 25% for CPS, 22 to 33% for DC, 25 to 50% for 30-Hz PDC, 42 to 58% for 60-Hz PDC, and 58 to 75% for AC. However, incidences of associated hemorrhages, except for DC (28%) were similarly high for all currents tested, including CPS (42–46%). In heterogeneous trials, Taube reported spinal-injury frequencies of 8% for CPS, 17% for DC, 25 to 58% for 20-Hz PDC, 33% for 30-Hz PDC, and 67% for 60-Hz PDC (output voltage was the same for all currents except CPS, for which it was doubled to elicit comparable responses). In the same one-on-one instream comparison discussed above regarding lethal effects, he reported spinal injuries for only 13% of the fish captured with CPS versus 47% for those captured with DC. Again, however, DC performed quite differently on another day in a one-on-one comparison with 25-Hz PDC–no spinal injuries versus 57%, respectively. Unfortunately, in these one-on-one boat electrofishing trials, catch rate was 56 to 68% lower for CPS than DC or 25-Hz PDC (relative peak output or field strength for the tested currents was not reported).

Like many of the above discussed investigators, Sharber et al. (1994) also documented fewer spinal injuries for large rainbow trout (>30 cm) collected with CPS, this time from the Colorado River in a comparison with simple square-wave PDCs with frequencies of 30 to 512 Hz. Incidence of injury with CPS was just 8% versus 24 to 62% for the simple PDCs. For further comparison, and as discussed above under "Waveform, Pulse Shape," 60-Hz, square-wave, quarter-sine, and exponential PDCs field-tested by Sharber and Carothers (1988, 1990), also in the Colorado River, resulted in injuries to 44 to 67% of the trout collected. As noted above under "Pulse Frequencies," Sharber et al. (1994) also reported an even lower incidence of injuries, just 3%, for 15-Hz PDC (6% duty cycle), but according to Sharber (personal communication), taxis at this frequency was unsatisfactory for effective electrofishing. Sharber (personal communication) noted that for a similar power output, CPS was also less effective than 60-Hz PDC, but that by increasing voltage for CPS by about 20%, a comparable response level could be obtained. In hatchery experiments, Sharber (personal communication) reported spinal injuries in 6% of trout exposed to CPS versus an average of 18% for those exposed to 60-Hz, square-wave PDC.

Combining data for the various field intensities in the same experiments discussed above with reference to immediate mortality, Meismer (1999) found that the incidence of brands on adult rainbow trout subjected to CPS (21%) was comparable to that for those subjected to DC (19%) or 15-Hz PDC (16%), but much less than that for those exposed to 60-Hz PDC (46%). However, if only treatments at the tetany level of field intensity are considered, incidences of branding were 60, 10, 40, and 75%, respectively. Again combining data for the various field intensities, incidences of spinal injuries for rainbow trout were insignificantly low for all treatment currents, but highest for CPS (5, 3, 1, and 1%, respectively). For comparable experiments with Colorado pikeminnow, Meismer (1999) reported no brands for any treatment and an incidence of spinal injury for CPS (6%) comparable to that for DC (6%) and 60-Hz PDC (5%) but somewhat less than for 15-Hz PDC (11%). Of these results, only the incidence of spinal injuries for Colorado pikeminnow exposed to 15-Hz PDC was significantly greater than that for controls (no injuries). All spinal injuries but one slight misalignment were minor. Associated hemorrhages were also assessed for Colorado pikeminnow (but not rainbow trout), but such injuries were insignificantly low for all treatment currents.

As discussed under "Pulse Frequency" above, Ruppert (1996) and Ruppert and Muth (1997) reported no vertebral damage for juvenile bonytail (5–8 cm TL) exposed to 10 s of homogeneous CPS or 30-, 60-, and 80-Hz PDCs at predetermined voltage-gradient thresholds for

taxis, narcosis, and tetany but variable results with respect to spinal or muscular hemorrhages (all class 2). Combining intensity-level treatments, CPS caused fewer hemorrhages than the PDCs (means of 8% means 10–19%, respectively). However, this trend was not always the case within intensity-level treatments–at the taxis level, incidence of spinal hemorrhages for CPS was similar to that for both 30- and 60-Hz PDCs (7%); at the narcosis level incidence of hemorrhages was again similar to that for 60-Hz PDC (10%) but greater than that for 30-Hz PDC (3%).

Muth and Ruppert (1996) have found that spawning razorback sucker are quite susceptible to electrofishing-induced spinal injuries and associated internal hemorrhages, but much less so with CPS than 60-Hz, square-wave PDC (4-ms pulses) at the same peak field intensity. They individually exposed several captive ripe males (50–55 cm TL) and females (55–60 cm TL) per treatment, for 10 s to homogeneous fields of the currents, each at a peak intensity of 1 V/cm (610 µS/cm; 20° C). Tetany was induced in all fish, but for those exposed to CPS, it was apparently incomplete since the fish continued to quiver during exposure (possibly the pseudo-swimming response). All fish expelled gametes during treatment, at least several hundred eggs by each female. No external hemorrhages or brands were observed, but subsequent necropsy and X-ray analysis revealed spinal injuries or associated internal hemorrhages in 50% of the fish (two males and two females) exposed to 60-Hz PDC and 14% (one female) of those exposed to CPS. Of the fish injured by 60-Hz PDC, the two males had class-3 hemorrhages above the spine slightly anterior to the dorsal fin, one female had a class-3 fracture slightly posterior to the dorsal fin and a class-2 spinal injury just beyond the anal fin, both with associated class-1 hemorrhages, and the other female had a class-2 hemorrhage above the spine slightly posterior to the origin of the dorsal fin. The female injured with CPS also had a class-2 hemorrhage also just behind the origin of the dorsal fin. No spinal injuries or hemorrhages were detected in control fish and no internal organ damage was observed for either treatment or control fish.

Sharber et al. (1994) suggested that despite the high frequency of pulses within each CPS train (intended to improve taxis), the reduction in the amount of electricity per unit time resulting from the spacing of those trains likely lessened the severity of myoclonic jerks and thereby the incidence of spinal injury relative to high-frequency PDCs. Reynolds and Kolz (1995) interpreted this "amount of electricity per unit time" as equivalent to duty cycle or percentage of "on time" per pulse or pulse train cycle, but Sharber et al. (1995) subsequently clarified "amount of electricity per unit time" to be that only during rapid changes in voltage at the beginning and end of pulses and not the full portion of time current was switched per unit time.

This is consistent with the observation discussed above under "Pulse Frequency" that spinal injuries probably occur with sudden changes in voltage differential as when current of sufficient intensity is switched on or off. However, other factors also appear to be involved in at least some pulse trains since CPS, with its three, quick, square-wave pulses delivered 15 times per second, effectively puts out a total of 45 pulses per second but generally results in injury rates comparable to or less than simple 15-Hz PDCs. Perhaps with respect to production of sudden muscular contractions resulting in spinal injuries, the effect of the three very rapid, 240-Hz pulses in each pulse train is physiologically comparable to a single pulse (see discussion of temporal summation of electrical stimuli under "Response to Electric Fields").

Pulse Duration, Duty Cycle

Neither of these interrelated factors have been adequately investigated to assess their effects on either electrofishing mortality or injury. The little evidence that does exist suggests no effect on mortality and a possible tendency for fewer spinal injuries using currents with longer pulses or greater duty cycles.

Collins et al. (1954) reported that under the conditions of their experiments, PDC pulse duration was not a lethal factor and that there was no direct relation between mortality and total energy applied per unit time (duty cycle). In controlled experiments on juvenile chinook salmon (5–11 cm TL) with homogeneous fields of 8-Hz, square-wave PDC, they found that fish exposed to a pulse duration of 20 ms (16% duty cycle) had the same mortality as those exposed to a pulse duration of 80 ms (64% duty cycle).

Lamarque (1990), suggested that pulse duration (as well as frequency) has a major effect on extent of injury and that pulse durations of 2 to 5 ms characterize some of the worst PDCs. Although pulse durations in this range are commonly used in PDC electrofishing, only one reviewed investigation, Taube (1992), addressed the effects of pulse duration or duty cycle on spinal injuries. However the experiments were limited and the overall results inconclusive. Some of Taube's (1992) results suggest a tendency towards fewer injuries among PDCs with longer pulse widths and higher duty cycles but other results suggest no relationship. Comparing incidence of spinal injury in large trout exposed to 5 s of heterogeneous 20-Hz PDC, he reported spinal injuries in 25% of the fish when using a duty cycle of 75% and pulse width of 38 ms and 58% of the fish when using a duty cycle of 25% and pulse width of 13 ms, but sample sizes were very small. When large rainbow trout were exposed instead for 5 s to

homogeneous fields of 30-Hz, square-wave PDCs with duty cycles of 50% or 72% (pulse widths of 17 or 24 ms respectively), incidences of spinal injuries and hemorrhages ranged from 33 to 58% without significant differences.

In commenting on the paper by Sharber et al. (1994; discussed above under "Pulse Frequency" and "Pulse Trains"), Reynolds and Kolz (1995) noted that when comparing results for tested 15-, 30-, and 60-Hz PDCs, it is possible to conclude that injury rates (3, 24, and 42%, respectively) increased with increasing duty cycle (6, 12, and 24%, respectively) as well as pulse frequency. But because injury rates among the three currents Sharber et al. (1994) tested with duty cycles between 10 to 12% were radically different (8% for CPS, 24% for 30-Hz PDC, and 62% for 512-Hz PDC), Reynolds and Kolz (1995) concluded that pulse frequency and the nature of the waveform (i.e., complex vs. simple PDC) are more important in this regard than duty cycle.

Voltage Spikes

As discussed earlier under "Electrofishing Currents and Waveforms," some electrofishing systems create positive voltage spikes (well beyond nominal peak voltage) at the leading (and) or trailing edges of pulses (or continuous current when it is switched on and/or off) and sometimes negative spikes or dips at the trailing end of pulses. Although a single, limited-scope investigation suggests that these waveform anomalies have little or no impact with respect to electrofishing injuries and mortality, the matter has not been adequately investigated and the effects on fish remain uncertain.

Sharber (personal communication) suggested that although the voltage of such spikes can be much higher than the designed peak voltage of the pulse, thereby dramatically increasing the magnitude of sudden voltage change at the leading or trailing edge of the pulse, the spikes are probably too short in duration to have a significant physiological or behavioral effect. In the only behavioral experiment on the effects of voltage spikes found for this review, Haskell et al. (1954) noted no significant improvement in the behavioral responses of fish subjected to a 1-Hz, square waveform (80% duty cycle) with a high initial peak (interpreted here as a spike) over that of fish subjected to a similar waveform without the high initial peak.

Hill and Willis (1994) conducted the only investigation of the adverse effects of a spiked PDC waveform. They used both a spiked square waveform described by Van Zee et al. (1996) and a similar unspiked waveform to electrofish hundreds of 20-cm-TL or larger largemouth bass in reservoirs of moderate to high conductivity (400 to 1,700 µS/cm) and temperature (16–25° C) and reported no immediate mortality and few brands for either waveform (fish were not X-rayed or necropsied).

The biological effects of voltage spikes, or lack thereof, remain inadequately documented. If voltage spikes are found to affect the incidence of spinal injury or have other harmful effects, it should be possible to electronically filter them out of the applied current (Novotny, personal communication).

Species

Evidence to date strongly indicates that trout, char, and probably salmon (subfamily Salmoninae) are generally more susceptible to brands, spinal injuries, associated hemorrhages, and probably mortality during electrofishing than most other fishes (Appendix B; Fredenberg, 1992—occurrences of spinal injury and/or hemorrhages reported as high as 98% for rainbow and cutthroat trout; Miskimmin and Paul, 1997a—concise review of injurious and lethal effects by species with tabulated summaries for 11 of 15 species of interest to the Province of Alberta; Paul and Miskimmin, 1997—review of effects and efficiency of electrofishing emphasizing selected species of interest to Alberta). In northern and upland regions of the north temperate zone, Salmoninae also are among the most frequently targeted species in electrofishing investigations. Data on the harmful effects of electrofishing on fishes other than the Salmoninae are limited and seldom comparable, but among species included in such reports and under at least some environmental and electrical-field conditions, burbot and sculpins (Cottidae) are particularly sensitive to electrofishing mortality and goldeye, some suckers (Catostomidae), channel catfish, largemouth bass, walleye, and possibly paddlefish are most sensitive to electrofishing-induced spinal injuries and associated hemorrhages. As discussed under "Effects Other Than Spinal and Related Injuries," mountain whitefish are at least sometimes especially susceptible to bleeding at the gills when subjected to electrofishing fields.

Mortality. Salmoninae appear to be more sensitive to electrofishing mortality than other fish taxa, but available data are few and seldom comparable. Only Meismer (1999) directly compared the lethal effects of selected currents at various field intensities for a salmonid, rainbow trout (33–60 cm TL), and a non-salmonid, Colorado pikeminnow (30–39 cm TL). Both species were similarly exposed to homogeneous 15- or 60-Hz, square-wave PDC, CPS, or DC with field intensity gradually increased to and held for 5 s at various levels from the threshold for twitch to 1 V_p/cm, a level sufficient to assure full tetany (530 µS/cm; 18° C). Only rainbow trout subjected to the highest intensity of 60-Hz PDC experienced immediate mortality (10%), but that mortality was reported to be insignificant

relative to controls (no mortality). In a separate laboratory comparison of the same two species with 10 s of 60-Hz, square-wave PDC or 60-Hz, quarter-sine wave PDC abruptly applied at a still higher field intensity (1.5 V_p/cm), Meismer (1999) again reported immediate mortality only for rainbow trout exposed to the 60-Hz, square-wave PDC, but this time at a significant 30%.

Only two investigations reported on relative susceptibility among species of Salmoninae) to electrofishing mortality. Pratt (1955) reported greater mortality for hatchery brown trout than brook trout or rainbow trout when exposed to either AC or DC. Although mortalities and injuries were very low among trout electrofished with AC, Hudy (1985) reported significantly greater mortality among rainbow trout than brook trout (but greater numbers of surviving fish with abnormalities, including spinal injuries, among brook trout).

Among non-salmonid taxa, there are several reports of very high immediate or short-term electrofishing mortality. Under rather extreme circumstances, Whaley et al. (1978; also Whaley, 1975) reported as much as 75 to 95% mortality for bluegill and fantail darter exposed for up to 3 min to PDC in laboratory experiments. However, some field operations can be just as lethal for certain species. Sculpins, according to Gowan (personal communication), are highly susceptible to extended tetany with flared opercules and subsequent mortality when captured in shallow riffles with outputs of 300 V or greater. Eloranta (1990) found burbot to be the most sensitive species to DC electrofishing mortality in the littoral zone of a lake in Finland. He reported that mortality for burbot was usually less than 25% but occasionally up to 50% when temperatures were high, whereas for other species, mortality was usually under 11%.

In contrast, most other investigators addressing the matter reported little or no electrofishing mortality among non-salmonids. Sorensen (1994) subjected spawning goldfish (32 female and 24 males) to 15 s of 100-Hz, square-wave PDC in an aquarium and reported recovery times greater than 10 min but no short-term mortality or brands. Cowdell and Valdez (1994) electrofished roundtail chub (22–40 cm TL) from the Colorado River with 40-Hz, square-wave PDC to check for electrofishing injuries and reported that all fish recovered quickly, typically in less than 60 s, with no immediate mortalities. Ruppert (1996) and Ruppert and Muth (1997) reported no mortalities among several hundred juvenile bonytail and humpback chub exposed for 10 s to homogeneous CPS or 30-, 60-, or 80-Hz PDC at intensities sufficient to induce taxis, narcosis or tetany. Walker et al. (1994) subjected juvenile northern pike to 10 to 60 s exposures of homogeneous AC and PDC at 0.4 to 2.1 V/cm (rms for AC, peak for PDC) and reported no mortalities within 16 to 24 h. However, 24 to 33% of the fish exposed to AC, but not PDC, had externally obvious cutaneous injuries along the entire length of the body (brands) or in the paired and median fins, and most of these (17–24%) failed to recover upright swimming within the 16 to 24-h monitoring period (survival beyond that time was not reported but most, if not all, of those fish would probably have died). Bardygula-Nonn et al. (1995) reported just 0 to 5% immediate to short-term (3-day) mortality for four centrarchids exposed to 30-, 60-, or 120-Hz PDC–zero for pumpkinseed, 5% for bluegill, 1% for smallmouth bass, and 1% for largemouth bass. Zeigenfuss (1995) reported no immediate mortality for several warmwater species collected with 60- to 80-Hz PDC, X-rayed for injury, and released back to Colorado Reservoirs (see discussion below regarding injuries). All fish immediately swam away upon release except some walleye which settled to the bottom for less than an hour before swimming away; no fish were retained and monitored for delayed mortality.

Injury. Relatively few investigations have directly compared the susceptibility of different species to electrofishing-induced spinal injuries and muscular hemorrhages, especially with or among non-salmonids. Frequencies of injuries reported for specific species are highly variable among and often within investigations and sometimes appear to be contradictory. Differences in rates and degree of injury, especially between investigations, are often difficult to attribute to species, fish size or condition, environment (including water conductivity and temperature), field intensity, or other current or field characteristics. For example, many recent studies report very high percentages of electrofished rainbow trout with spinal injuries and hemorrhages (Appendix B), but McCrimmon and Bidgood (1965) reported no skeletal damage attributable to either AC or PDC fields among 80 hatchery rainbow trout (11–26 cm TL) that were experimentally exposed in the laboratory or among 291 wild rainbow trout (6–59 cm TL) that were electrofished in Ontario streams tributary to the Great Lakes. All fish were X-rayed (the hatchery fish before and after exposure), and some were dissected. Dwyer and White (1995) also reported no spinal injuries among 44 X-rayed rainbow trout, including 4 mortalities, exposed to high-frequency PDC (20 were examined 35 days after treatment, the rest were frozen immediately or within 24 h of treatment).

Still, most existing data support Salmoninae as the fish taxa most susceptible to electrofishing injury. In one investigation, Fredenberg (personal communication) found spinal injuries in 2 to 20% of rainbow trout captured with DC, 15-Hz PDC, or CPS, but only 0 to 2% of mountain whitefish, white sucker, or longnose sucker captured with the same currents. When specimens with only hemorrhages along the spine or associated musculature (all minor) were added to these figures, the percentages of injured fish increased to 6 to 42% for rainbow

trout, 2 to 29% for mountain whitefish, and 4 to 18% for the suckers. In addition to his investigation of impacts on rainbow trout, Zeigenfuss (1995) X-rayed and released several warmwater species collected in three Colorado reservoirs and concluded that warmwater species (see details below) are less vulnerable to spinal injuries than rainbow trout. Also, for contaminants analysis, Krueger (personal communication) dissected several electrofished species, including common carp, suckers, walleye, northern pike, and black basses, but recalled only seeing substantial numbers of spinal injuries among trout.

Only Kocovsky et al. (1997) and Meismer (1999) reported greater frequencies of electrofishing injuries for non-salmonid than salmonid species. In a comparative 3-year field study also referenced below with regard to salmonids only, Kocovsky et al. (1997) reported greater percentages of old, externally detectable spinal injuries in longnose sucker (7–13%) than in rainbow trout or brook trout (2–6%) or, for two of three years, brown trout (3–12%). In laboratory experiments discussed above with regard to lethal effects, Meismer (1999) also directly compared the injurious effects of the selected currents (DC, 15- or 60-Hz PDC, or CPS) and field intensities (gradually increased from zero to the thresholds for twitch, taxis, or narcosis, or to 1 V_p/cm to assure full tetany) on rainbow trout (33–60 cm TL) and Colorado pikeminnow (30–39 cm TL). When data for all treatments were combined (n = 320/species), 26% of the rainbow trout suffered brands and just 3% suffered spinal injuries, whereas none of the Colorado pikeminnow suffered brands but 7% suffered spinal injuries. All spinal injuries were minor (class 1) except for a slight misalignment in one Colorado pikeminnow. In a separate comparison of the effects of the same two species abruptly exposed to 10 s of 60-Hz, square-wave PDC or 60-Hz, quarter-sine-wave PDC at a still higher field intensity (1.5 V_p/cm), Meismer (1999) reported even higher percentages of rainbow trout with brands (73% for combined treatments; n = 40/species) and 10% with spinal injuries, all minor. No Colorado pikeminnow in these higher-intensity, abrupt-exposure treatments suffered brands or spinal injuries.

Among the Salmoninae, particularly rainbow, brook, and brown trout, there is no consistent ranking regarding susceptibility to electrofishing injury. Although Hudy (1985) observed few injuries among trout captured with AC, he reported significantly greater numbers of surviving fish with abnormalities, including spinal injuries, among brook trout than among rainbow trout (but, as noted above, greater mortality among rainbow trout). Fredenberg (1992) generally found rainbow trout (and probably cutthroat trout) more susceptible to spinal and related injuries than brown trout. Data reported by Meyer and Miller (1991, unpublished manuscript, 1991; Wyoming Game and Fish Department, 1991) indicated the same for fish in stream sections electrofished four times in succession with 40-Hz, square-wave PDC but the reverse for stream sections electrofished only once. However, differences between species in the latter reports were not statistically significant (Meyer, personal communication), and when stream sections were fished only once with Coffelt's CPS current, incidences of injuries were similar for rainbow trout and brown trout. Kocovsky et al. (1997), using three-pass depletion electrofishing with 100-Hz PDC, found that incidence of externally detectable (old) spinal injuries increased progressively for three successive years in an annually sampled stream segment and that the frequency of these injuries was greater for brown trout (3–12%) than rainbow or brook trout (2–6%). Comparing incidences of spinal injuries and hemorrhages for rainbow and brown trout electrofished with 60-Hz, half-sine PDC in three Colorado Rivers, Thompson (1995) and Thompson et al. (1997a) reported highest and lowest percentages for rainbow trout (e.g., 6 and 64% for spinal injury, 13 and 76% combined with muscular hemorrhages), but rank in susceptibility relative to brown trout varied with river, electrofishing technique (boat with throwable anode vs. shore-based wading with multiple anodes), and field intensity near the anodes.

Several investigations, in addition to a couple mentioned above, compared incidences of electrofishing injuries among species other than Salmoninae. Spencer (1967a) reported up to 16% spinal injury among experimentally electrofished bluegill but almost none among largemouth bass. Clady (1970, according to Schneider, 1992) reported some injury to smallmouth bass and white sucker with 560-volt AC gear, but Schneider (1992) did not specify whether these were spinal or other injuries or compare percentages. Holmes et al. (1990) documented 12.5% spinal injury for northern pike, zero to 18% (but less severe) injury for Arctic grayling, and no injury for humpback whitefish and least cisco. Fredenberg (1992) reported only one minor injury for Arctic grayling and no injuries among small numbers of sauger. In a cursory investigation of the injurious effects of DC and PDC, Gardner (1992, according to Grisak, 1996) found only hemorrhages, no spinal injuries, among shocked and control smallmouth bass and channel catfish and only one injury among shocked paddlefish he X-rayed and necropsied.

Bardygula-Nonn et al. (1995) investigated the lethal (discussed above) and injurious effects of 30-, 60-, and 120-Hz PDC on bluegill, pumpkinseed, smallmouth bass, and largemouth bass collected from lakes with conductivities of 122 to 789 µS/cm. Fish were monitored for 3 days after capture. Fish that died, fish with severe external injuries, and 25% of the normal appearing survivors for each species were X-rayed and necropsied. Brands (external ecchymoses, as described by the authors) were found on most fish that died (0–5%

depending on species), but few others. Spinal injuries were observed only in one bluegill mortality and all six largemouth bass that died and were limited to partial separations (subluxations) or misalignments; vertebral fractures and presumably compressions were not detected. Internal soft-tissue damage and hemorrhages were found in fish that died within 3 days and in 14% of the smallmouth bass and 2% of the largemouth bass survivors that were sacrificed and necropsied; none were observed in bluegill or pumpkinseed survivors that were similarly examined.

Zeigenfuss (1995) X-rayed and released several warmwater species collected in three Colorado reservoirs during June or July by boat electrofishing with 60- to 80-Hz PDC. Among these fish, walleye and largemouth bass appeared to be most vulnerable with incidences of spinal injury ranging from 0 to 21% (18% overall) and 0 to 33% (12% overall), respectively. Other species for which spinal injuries were observed included common carp (8% injured), bluegill (1 of 6 fish), and yellow perch (1 of 12). No injuries were observed among one white sucker, two freshwater drum, six white crappie, and one black crappie. All spinal injures documented by Zeigenfuss (1995) for these warmwater species were limited to compressions (class 1); no misalignments or more serious injuries were observed.

As discussed earlier under "Nature of the Injuries" and "Type of Current—Injury," Grisak (1996) compared the injurious effects of DC and 40-Hz PDC for several species of warmwater fishes electrofished from the Missouri River in Montana. All fish succumbed to tetany but revived within minutes of capture and no brands were observed. Goldeye were the predominate species taken with each current, the only species injured under DC (perhaps because of unusually strong taxis), and the species suffering the greatest incidence of hemorrhages under PDC. Among goldeye, incidences of spinal injuries, muscular hemorrhages, and either or both types of injury were 21, 21 and 32%, respectively, for DC, and 4, 39, and 43%, respectively, for PDC. Electrofishing injuries for other species were observed only among those collected with PDC. River carpsucker (30–58 cm TL) were the next most susceptible species with 18% experiencing spinal injuries and 9% experiencing hemorrhages (27% total, none with both types of injury). Among the remaining fishes collected with both currents (but injured only by PDC), 8% of flathead chub (11–24 cm TL) incurred spinal damage and 5% of shorthead redhorse (18–49 cm TL) incurred hemorrhages. Small numbers of longnose sucker (including fish 43–49 cm TL) and freshwater drum (30–43 cm TL) were captured only with PDC, but no injuries were detected. Several adult sicklefin chub and sturgeon chub captured by trawl were placed in a plastic bucket with holes and subjected to 10 s of up to 0.18 V/cm about a meter from the anode. Grisak (1996) reported no obvious spinal damage or hemorrhages for either species but noted that the results should be considered inconclusive because injuries in such small fish are difficult to detect. All vertebral injuries in captured fish were class 1, except for a solitary class-2 injury in a river carpsucker, and involved 3 to 9 vertebrae. Hemorrhages were half class 1 and half class 2. Among controls collected by other means and also X-rayed and necropsied, Grisak (1996) reported only one fish (a goldeye) with a fresh internal injury, a spinal compression.

In laboratory experiments, Ruppert (1996) and Ruppert and Muth (1997) reported hemorrhages associated with the spine for 7% of juvenile bonytail and 20% of juvenile humpback chub exposed to homogeneous CPS at tetany-level intensity, but the difference was not statistically significant. For juvenile bonytail similarly subjected to 30-, 60-, or 80-Hz PDC at homogeneous field intensities sufficient to induce taxis, narcosis, or tetany, incidences of such hemorrhages ranged from 3 to 27%. No immediate mortalities, external injuries, or vertebral damage (based on dissection and low-power microscopic examination) were observed for either species. Among controls, only one humpback chub had a muscular hemorrhage at or near the spine.

Remaining reports of electrofishing injuries for fishes other than Salmoninae were based on single-species investigations or observations. Spencer (1967a) reported substantial occurrences of injury for channel catfish (at least 6 of 10) electrofished in a pond with 3-phase AC. Newman (1992, unpublished manuscript, 1991) reported up to 31% injury for walleye. Roach (1992) reported injuries in 5 to 28% of northern pike exposed to homogeneous 30- to 120-Hz PDC; however, he noted (Roach, personal communication) that the injuries were much less obvious and less serious than those usually observed in trout. Among 40 roundtail chub taken from the Colorado River with 40-Hz PDC, Cowdell and Valdez (1994) reported rapid recovery, no abnormal swimming behavior, no brands or external hemorrhaging, no signs of spinal injury based on lateral X-rays, and only 5% with internal hemorrhages based on fillets along the spine (classes 2 and 3). They also noted that external signs of injury (including brands, abnormal swimming, and bleeding at the gills) were rarely observed in native cyprinids they had electrofished from the Colorado River in other investigations.

Among teleosts in North America, catfishes (order Siluriformes, mostly Ictaluridae) may be relatively unique in their sensitivity and reaction to electric fields (Morris and Novak, 1968; Corcoran, 1979). Their lateral-line system includes electroreceptors (Peters and Buwalda, 1972; Kramer, 1990), which may account for their ease of capture with extremely simple and low voltage devices, some of

which are illegal in certain states (McSwain, 1988). In support of these observations, Jesien and Hocutt (1990) found 50% tetany voltage-gradient thresholds for channel catfish to be generally much lower than reported for other species at comparable water conductivities. However, Edwards and Higgins (1973) reported stun thresholds for 22- and 28-cm channel catfish that differed little from those for 15-cm bluegill and were slightly greater than for 41-cm bowfin when using 10- to 200-Hz, square-wave PDC; 100-Hz, exponential PDC; and a 100-Hz, square-wave pulse train delivered at 25 Hz. Stun thresholds for the catfish were substantially lower than for the smaller bluegill only when using DC (but still slightly greater than for the bowfin) and were actually much higher than for either the smaller bluegill and larger bowfin when using 25-Hz, exponential PDC. As noted earlier under "Comparison of Currents for Electrofishing Purposes," Pugh and Schramm (1998) found flathead catfish and blue catfish generally much more susceptible to capture using 15-Hz than 60-Hz PDC, but channel catfish generally more susceptible to 60-Hz PDC. Aside from Spencer's (1967a) observations of high incidence of spinal injuries for channel catfish (noted above) and Edwards and Higgins' (1973) observation that channel catfish recovered quickly from electrical immobilization with few mortalities, the adverse effects of electrofishing on catfish have not been studied. Likewise for any relationship between susceptibility to electric fields and the presence of special electroreceptors.

The Chondrostei, sturgeon, and paddlefish also have electroreceptors. Whether these fish are also more sensitive to electric fields than most other species has not been reported. Fredenberg (1992) reported no injuries among small numbers of electrofished shovelnose sturgeon. Berg (1982, according to Grisak, 1996) who visually surveyed over a 1,000 paddlefish after electrical agitation in the Missouri River, Montana, reported only two mortalities, both with ruptured notochords (voltages may have been excessively high and pulse frequencies were as high as 120 to 160 Hz). Gardner (1992, also according to Grisak, 1996) reported only one spinal injury among paddlefish he experimentally exposed to PDC. However, according to Pfeifer (personal communication), paddlefish electrofished with PDC in the Yellowstone and Missouri Rivers were highly susceptible to spinal injuries despite their cartilaginous endoskeletons and lack of vertebral centra. Necropsy of those fish revealed, as per Berg (1982) above, that their notochords were badly ruptured.

Size

As discussed earlier (see end of section on "Response Thresholds"), fish generally become more sensitive to electric fields (i.e., respond at lower field-intensity thresholds or, in heterogenous fields, at a greater distance from the electrode) as size increases, at least up to some point beyond which size appears to no longer matter. Accordingly, since electrofishing mortality is at least partially dependent on field intensity and spinal injuries appear to occur with sudden changes in voltage differential beyond some threshold level, larger fish might be expected to be more susceptible to electrofishing mortality and injury than smaller fish, but experimental and field data either fail to support these relations or do so inconsistently. With respect to mortality, this relation might only exist with increasing exposure time, and some researchers have even reported greater electrofishing mortality for smaller fish. With respect to spinal injuries, the anticipated relation has been supported by some experimental and field research but not by others.

For fish of a particular species, similarly oriented in an electric field (e.g., parallel to the lines of flux), Collins et al. (1954) and Whaley (1975) concluded that the increase in mortality attributed to field intensity appears to be unaffected by fish length whereas that attributed to exposure time increases with fish length. Collins et al. (1954), exposed fingerling chinook salmon in four size groups of about 5, 7, 9 and 11 cm TL to 30 s of homogeneous 2-Hz PDC (48 μS/cm, 10–20° C) with fish held parallel to the lines of current and reported that similar field intensities (about 12.5 to 15 V/cm) were required to kill 50% of the fish in each size group. However, as a corollary, there is a direct relation between fish size and the total voltage across the fish required to kill that fish (head-to-tail voltage differential = voltage gradient x fish length). Plotting their data for corresponding head-to-tail voltages, Collins et al. (1954) found that to kill 50% of the fish, 60 V was required across 5-cm salmon and 140 V across 11-cm salmon. Whaley (1975) subjected similar-size subgroups of 3- to 8-cm fantail darters and 9- to 17-cm bluegills to 2-, 9-, and 16-Hz PDC at 3 to 5 V/cm for 5 to 180 s (154 μS/cm, 10° C) and also reported that increased fish length further increased mortality as exposure time was increased but not as field strength was increased. In fields of fixed intensity, Collins et al. (1954) determined that increased fish length also further increased mortality as either pulse frequency or water temperature was increased. However, Whaley (1975) and Whaley et al. (1978) reported no significant effect of fish length on mortality attributed to pulse frequency.

Contrary to expectations based on the above discussed work, Habera et al. (1996) and Bardygula-Nonn et al. (1995) actually found greater electrofishing mortality among fish under rather than over 10 cm TL. Habera et al. (1996) used three-pass depletion AC in a very-low conductivity stream and reported 15 to 23% mortality in rainbow trout measuring 5 to 9.9 cm TL and 2 to 9% mortality in trout measuring 10 to 23 cm TL. Thirteen of the 20 mortalities on which these figures were based had

not been recovered and were assumed to have died. If they escaped or were preyed upon rather than having died, electrofishing mortalities would have been reduced to 5 to 10% and 2 to 4%, respectively. Bardygula-Nonn et al. (1995) reported 5.3% mortality among 568 bluegill electrofished in lakes with 30-, 60-, or 120-Hz PDC but that mortality was proportionately greater among specimens less than 10 cm TL than among larger specimens.

Unlike mortality, many researchers have documented a positive relation between increasing fish size and incidences of spinal injuries and hemorrhages in tissues near the spine. McMichael et al. (1991; also McMichael and Olson, unpublished manuscript, 1991) subjected 14- to 48-cm-FL rainbow trout to DC and 30- and 90-Hz PDC in hatchery raceways and reported a significant positive correlation between fish length and occurrence of spinal injuries and major hemorrhages (but not minor hemorrhages). Similarly, Hollender and Carline (1994) reported that the incidence of injury among AC and PDC-electrofished brook trout increased with size from 14% for fish 9 to 13 cm to 26% for fish 13 to 17 cm and 42% for fish 18 to 24 cm. Habera et al. (1996) found that, contrary to lethal effects, rainbow trout greater than 10 cm TL incurred significantly more spinal injuries or hemorrhages than smaller fish (0–15% for fish 10–23 cm TL and 0% for fish 5–9.9 cm). Thompson (1995) and Thompson et al. (1997a) extensively modeled the relationship between size and incidences of spinal damage or hemorrhages for rainbow trout (13–51 cm TL) and brown trout (10–49 cm TL) electrofished with 60-Hz PDC from three Colorado rivers and concluded that in most cases longer fish had a higher probability of injury.

Combining data for wild rainbow trout captured with DC, 60-Hz PDC, and a hybrid of the two currents (Fig. 5J), Dalbey et al. (1996, also Dalbey, 1994) also found a tendency for increased incidences of spinal injury with increased size from 27% for 15- to 20-cm trout to 45% for 33- to 35-cm fish. Within this size range, incidences of spinal compressions only (class 1 spinal injury, Table 3) generally decreased with increasing size from 23% for 15- to 18-cm trout to 0% for 33- to 35-cm fish, whereas incidences of spinal misalignment and compression (class 2) generally increased from 5% for 15- to 18-cm trout to 30% for 30- to 33-cm fish but then dropped to 11% for 33- to 35-cm fish, and incidences of vertebral fractures or complete separation of two or more vertebrae (class 3) increased from zero for 15- to 18-cm specimens to 8 to 11% for 25- to 33-cm fish, then rose to 35% for 33- to 35-cm fish.

Data supporting the relation for non-salmonid fishes are more limited. Among northern pike 36 to 74 cm FL that were subjected to similar electric fields, Roach (1992) found that those fish experiencing spinal injuries were significantly larger ($\bar{x}$ = 57 cm) than those that were not injured ($\bar{x}$ = 51 cm). Newman (unpublished manuscript, 1991) noted that size might be a factor for walleye, but his sample size (30 specimens, 18–48 cm) was too small and variable to be conclusive.

Other researchers have reported no relation or inconsistent relations between fish size and incidences of injury. Zeigenfuss (1995) compared injury rates among five size classes of rainbow trout subjected to 60-Hz PDC and in his first-year trial found that the smallest group (15–27 cm) had significantly fewer spinal injuries (~52%, Zeigenfuss, 1995–Fig. 1) than the four larger-size groups (27–35 cm; ~65–75%) for which differences in mortality were not significant. In a second-year trial with higher field intensity, Zeigenfuss (1995) reported that spinal-injury rates were nearly equal for all size groups. Similarly, in extensive surveys of spinal injuries among salmonids, neither Meyer and Miller (1991, unpublished manuscript, 1991; also Meyer, personal communication) nor Fredenberg (1992) found an overall relation between the percentage of injured fish and size. Zeigenfuss (1995) also X-rayed and released several warmwater species collected in three Colorado reservoirs during June or July by boat electrofishing with 60- to 80-Hz PDC. Based on the capture of fish averaging 15 to 45 cm TL, he reported that there was no evidence that larger warmwater fish were generally more vulnerable to injuries than smaller fish. Among species collected in greater numbers, mean length of injured fish was greater than for uninjured fish only for largemouth bass.

Condition

The physical condition of fish subjected to electric fields can affect their susceptibility to electrofishing injury and mortality, but assessment of this factor is based mostly on suppositions and casual observations rather than specific experiments and data. It is logical to expect that fish in poor health, or an otherwise highly stressed condition (as when habitat approaches upper limit temperature or lower limit oxygen conditions), might be less alert and sensitive to electric fields, thereby responding less strongly and reducing chances for spinal injury, but they also would be less able to withstand the stresses of tetany and apnea during narcosis, thereby increasing probability of death. Thompson et al. (1997a) observed higher incidences of injury among populations of rainbow trout with generally higher condition factors and suggested that better-condition wild fish may be more likely to be injured because of more powerful muscular contractions. However, whether in poor condition or otherwise normal, fish with weakened or brittle bones, particularly vertebrae, may be especially susceptible to spinal injuries. Stewart (1967, as cited by Lamarque, 1990) suggested that spawning fish, particularly salmon, may

be especially susceptible to spinal injuries due to skeletal decalcification; likewise for fish with diets deficient in magnesium and calcium (Lamarque, 1990). Over-wintering fish may be less likely to suffer either spinal injuries or mortality due to thermally reduced metabolism and slowed responses, but like most of the above, this hypothesis has not been experimentally tested.

Repeated Exposures

If there are significant adverse impacts on fish resulting from single events, lethal or otherwise, the effects of multiple electrofishing events should at least be cumulative. Hypothetically, fish that do not fully recover between events may be more susceptible to harmful effects in subsequent exposures, thereby compounding those impacts. Conversely, they may be physiologically unable to respond as strongly to subsequent exposures, thereby reducing expected cumulative effects. If electrofishing events are sufficiently spread to allow full physiological recovery, fish may learn from the experience and be more apt to escape less effective portions of the field in subsequent events, although they may still be injured by the exposure. However, investigations of lethal effects (only two) have demonstrated no short-term differences in mortality over controls and suggest that stress of repeated handling may have a greater impact on delayed mortality. On the other hand, and as might be expected, investigators of injurious effects have documented cumulative increases in the incidence of injuries among fishes inhabiting repeatedly sampled waters, not only during multiple-pass sessions, but in successive sessions or years of sampling. In doing so, they also documented past injuries among fish that either were missed by netters or escaped at the fringes of the effective field during earlier passes, sessions, or years. Stress and injury caused by repeated exposures to electric fields might also affect short and long-term growth and condition of fish (see later discussion on "Effects on Growth and Condition").

Barrett and Grossman (1988) studied the effects of repeated electrofishing events on survival of mottled sculpin (4–8 cm SL) and reported no significant differences between treatment and control fish. They exposed mottled sculpin for 30 s to DC fields weekly, five times over a 4-week period, in an outdoor artificial stream (low conductivity, 12–14° C). Controls were initially collected by kick-netting and both control and treatment fish were handled after each electrofishing event. Cumulative mortalities increased progressively with exposure-handling events and time and by the end of the experiment ranged from 35 to 60% for treatment fish and 45 to 50% for controls. Barrett and Grossman (1988) concluded that repeated-handling stress had a greater impact on cumulative mortality of mottled sculpin than repeated DC electrofishing.

Eloranta (1990) exposed 3- to 30-cm burbot, ruffe, and bullhead to 20 s of 550-V DC at about 15 to 20 cm from the anode on each of 10 consecutive days to assess the lethal effects of repeated exposures. During those 10 days, he, like Barrett and Grossman (1988), observed no differences in short-term mortality between the experimental groups and controls and concluded that delayed effects were minimal.

Meyer and Miller (1991, unpublished manuscript, 1991) reported nearly four times as many spinal injuries (30% vs. 8% based on X-rays) among previously uncaptured rainbow and brown trout (14–40 cm TL) collected during the last pass of a four-pass, 2-week population estimate than among trout collected in a single-pass operation in an upstream portion of the same stream (340–350 µS/cm; 7–8° C). They concluded that many of the unmarked (not previously captured) trout taken in the fourth pass had suffered some injuries during prior passes.

Habera et al. (1996) assessed injury among rainbow trout (5–23 cm TL) electrofished with 60-Hz AC in a three-pass depletion population estimate in a southern Appalachian stream (14 µS/cm, 15° C). No spinal injuries or hemorrhages were detected among mortalities (3%) or 12 angled controls examined by X-ray or necropsy, but among a subsample of electrofished survivors, 3% incurred class-2 spinal injuries and another 3% class-2 hemorrhages (6% combined). The injured fish were greater than 10 cm TL (12–17 cm) and collected only in second and third passes (fish taken during these passes may have been shocked but not captured in the preceding pass or passes). No external injuries (e.g., brands or erratic swimming behavior) were observed among survivors not X-rayed and necropsied.

Kocovsky et al. (1997) evaluated the injurious effects of annual three-pass-depletion electrofishing (for population estimates) on salmonids and longnose sucker in three small, low-conductivity (34–63 µS/cm), streams. Prior to this 3-year investigation, study reaches had been annually electrofished for 5 years, and biologists noted that a significant proportion of the fish had spinal deformations and related anomalies. Electrofishing, as in the past, was conducted by wading with backpack units (hand-operated anode and trailing cathode screen) using 100-Hz, square-wave PDC with a 50% duty cycle. As controls for two streams, Kocovsky et al. (1997) also single-pass sampled stream segments that were not believed to have been previously electrofished. Sampling was conducted in mid-to-late summer with maximum water temperatures of 12 to 18° C. Over 8,000 yearling and older fish were examined visually and by touch for externally evident anomalies suspected to represent healed spinal injuries from prior years of three-pass sampling (and probably the more severe of new injuries). For brook trout in two

streams, they found no significant difference in incidence of externally detectable injuries between streams but significant differences among years and between three-pass study and single-pass control reaches. Incidences of detected injuries in three-pass segments progressively increased from one year to the next—5% and 4% in the first study year, 12% and 11% in the second year, and 14% and 23% in the third year. Incidences of injuries for single-pass control segments of the two streams were much lower and remained low in all three years—zero in the first year, 2% and 0% in the second year, and 1% and 3% in the third year. In the third stream, detected injuries in three-pass electrofishing study segments also increased annually from 2 to 6% for brook trout and rainbow trout and 3 to 12% for brown trout, but not for longnose sucker in which externally detected injuries first increased from 9 to 13%, then fell to 7% in the third year. They also found that externally detectable injuries represent only a relatively small proportion of total spinal injuries; 44% of 114 captures not showing external signs of old spinal injuries had spinal injuries that could only be detected by X-ray (or necropsy). Kocovsky et al. (1997) concluded that electrofishing-induced spinal injuries in salmonids and longnose suckers can accumulate over time in stream segments that are sampled annually by intensive electrofishing.

Summary

Factors considered in the literature to affect electrofishing injuries and mortalities include type of current, field intensity, duration of exposure, orientation of fish relative to lines of current, and for AC and PDC, waveform characteristics such as shape, wave or pulse frequency, and pulse width; also, fish species, size, and condition. However, data regarding the effects of these factors are sometimes sparse, difficult to compare, and often questionable.

Available data generally support the contention that of the three types of electrofishing currents, AC is most harmful, DC least, and PDC usually somewhere between depending on the frequency and complexity of pulses. Although there are reports of no mortality or injury for each type of current, when such adverse effects do occur and comparisons are possible, AC tends to be more lethal than either DC or PDC, and AC and moderate to high-frequency PDC tend to cause more spinal injuries and hemorrhages than DC, low-frequency PDC, or the CPS pulse train (a complex PDC). The extent of mortality or injury caused by each of these currents varies considerably with how they are used, other electrical parameters, biological factors, and environmental conditions. With enough field intensity and duration of exposure, any type of current can be lethal, and under certain conditions even DC can injure substantial numbers of fish.

As for most chemical substances and physical parameters affecting living organisms, concentration (in this case, field intensity) and duration of exposure are the primary factors determining the physiological stressfulness and lethality of electrofishing currents on fish. Beyond lethal threshold levels, increases in electrical-field intensity or duration of exposure typically result in increased mortality. However, it is not field intensity itself, but the magnitude of voltage differential it generates across fish (usually head-to-tail voltage) or specifically affected nerves or tissues that causes electrofishing mortalities and most sublethal physiological effects and behavioral responses. That voltage differential is a function of both field intensity and orientation of the fish relative to the lines of current.

Unlike their crucial roles in electrofishing mortality, field intensity beyond requisite threshold levels has an unclear but certainly not critical effect on electrofishing-induced injuries, and exposure time does not appear to be important except when using PDC. Spinal injuries and associated hemorrhages can occur in fish located anywhere in the field at or above the intensity threshold for twitch in the zone of perception. Among fish injured in the zone of perception, as many are likely to escape as move into the effective portion of the field for capture.

The principal cause of spinal injuries appears to be muscular convulsions (myoclonic jerks or seizures) induced by sudden changes in field intensity or, more specifically, in voltage differential across the fish or affected tissues at or above the relatively low threshold in magnitude of change for twitch. Such sudden changes occur when current is switched on and off or pulsed, when fish leap frantically out of and back into the electrified water, and when netted fish are removed from or dipped in and out of the field. Accordingly, duration of exposure in DC should have no effect on incidences of spinal injuries while fish remain in the water, but in PDC, longer exposures subject fish to more pulses and thereby increase potential for spinal injury. However, neither muscular convulsions as the principal cause of spinal injuries in fish nor sudden changes in voltage differential as the principal cause of the convulsions have been experimentally documented. Also, the latter seemingly is contradicted by the observation of twitches during uninterrupted DC and occasional documentation of as many spinal injuries (at least minor ones) in DC with just two sudden change events (when the current is switched on and later off) as in some simple or complex PDCs with numerous sudden changes in voltage differential.

Increases in spinal injuries with exposure time might be expected as well for AC with its cyclic changes in voltage differential and direction (effectively alternating half-sine pulses), but limited experimental evidence suggests otherwise. Perhaps the changes in AC voltage are not sufficiently sudden (if so, the same would apply to half-sine PDC), or the change in direction precludes possible consecutive-pulse summation effects that might sometimes be necessary to achieve the threshold magnitude of change in voltage differential.

Whether the probability or degree of spinal injuries and hemorrhages increases with field intensity or not, fish in a state of narcosis (petit mal) or tetany (grand mal) may no longer be subject to the sudden convulsions that are believed to cause most spinal injuries in PDC (and possibly AC). Injuries might still occur during transition between these states and when fish are removed from the field. If some spinal injuries do occur during tetany, as has long been suspected but unproven, the sustained muscular tension would have to be sufficiently strong to permanently compress one or more portions of the spinal column, burst blood vessels, and possibly fracture vertebrae. Aside from this possibility, and unlike severe stress, fatigue, and mortality, measures to specifically reduce the intense zone of tetany around an electrode might not have much impact on the frequency of spinal injuries.

Orientation of fish when first exposed to the effective portion of the field is probably as significant a factor in electrofishing injuries as in other responses and mortality. However, based on limited evidence, greatest effect appears to occur when fish are perpendicular to rather than parallel to the lines of current (minimum rather than maximum head-to-tail voltage differential). If so, experiments to assess the injurious effects of electric currents on fish might be confounded or biased to minimum effects if fish are held parallel to the direction of current.

Pulse frequency appears to be a primary factor affecting the incidence of spinal injuries in PDC and may be a significant secondary factor in electrofishing mortalities. As expected if spinal injuries are caused primarily by sudden changes in electrical potential, the incidence of injuries is generally lowest for low-frequency currents and increases with pulse frequency. With regard to incidences of spinal injuries, the CPS pulse train with a primary frequency of 15 Hz appears comparable to simple low-frequency currents (and DC). It is unknown whether other pulse trains or complex variations of PDC also result in as few injuries as low-frequency PDCs.

The effects of pulse shape or waveform, pulse width or duty cycle, and voltage spikes on mortality and spinal injuries have been inadequately investigated and data that are available are difficult to compare and sometimes contradictory. Although exponential and half-sine PDCs have been implicated as particularly lethal and half-sine, quarter-sine, and square PDCs as particularly injurious, the effects of PDC waveforms on electrofishing mortality and injury remain inconclusive. Likewise for AC waveforms, despite one comparison of sine-wave and triangular-wave AC which revealed no significant differences in incidence of externally obvious injuries but notable differences in the nature and perhaps severity of those injuries. The little data that exists with regard to pulse duration or duty cycle suggests no effect on mortality and a tendency for fewer spinal injuries using currents with longer pulses or greater duty cycles. A limited-scope investigation suggested that voltage spikes have little or no impact on electrofishing injuries or mortality.

Evidence to date strongly indicates that Salmoninae (trout, char, and salmon) are more susceptible to spinal injuries, associated hemorrhages, and probably mortality during electrofishing than most other fishes. Among other species, burbot and sculpins (Cottidae) were reported to be particularly susceptible to electrofishing mortality, at least under some environmental and electrical-field conditions, whereas goldeye, some suckers (Catostomidae), channel catfish, largemouth bass, walleye, and possibly paddlefish were reported to be more susceptible to electrofishing-induced spinal injuries and associated hemorrhages. Electrofished mountain whitefish have been reported to be particularly susceptible to bleeding of the gills.

Because voltage differential across fish or specific tissues increases with size, larger fish have been expected to be more susceptible to electrofishing mortality and injury than smaller fish. However, laboratory and field data suggest that increases in electrofishing mortality with size might only occur with increases in exposure time and some researchers have reported greater electrofishing mortality among smaller fish. Some data support an increased frequency of spinal injuries as fish size increases, but other data do not, and so the importance of size remains questionable.

The physical condition of fish can affect their susceptibility to electrofishing injury and mortality, but assessment of this factor is based mostly on suppositions and casual observations rather than specific experiments and data. Fish in poor health may respond less strongly to electric fields, thereby reducing chances for spinal injury, but they also may be less able to withstand the stresses of tetany and apnea during narcosis, thereby increasing probability of death. On the other hand, weakened skeletal systems probably make fish especially susceptible to spinal injuries. Temperate fishes electrofished during late fall through early spring may be less likely to

suffer either spinal injuries or mortality due to lower water temperatures that substantially reduce metabolism and slow responses.

If there are significant harmful impacts on fish resulting from single electrofishing events, the effects of multiple events should be cumulative. In at least some cases, the stress of repeated handling has greater impact on delayed mortality than repeated exposures to electric fields. The incidence of total injuries among captured fishes inhabiting repeatedly sampled waters increases cumulatively, not only during multiple-pass sessions, but in successive seasons or years of sampling. Some newly captured fish may have been injured during prior treatments or sampling but at that time either escaped the effective portion of the electric field or were missed by netters.

Effects on Long-Term Survival

Most investigations suggest that long-term survival (that beyond a week or two) is seldom significantly affected by electrofishing. Apparently, most electrofishing mortality occurs immediately or shortly after capture as a result of asphyxiation or severe physiological stress. Also, if not too severe, most fish survive spinal injuries caused by electrofishing (see discussion under "Relation between Mortality and Injury"). Still, there is some evidence that injury or severe stress in fish as a result of exposure to electric fields can result in long-delayed as well as short-term or intermediate-term mortality.

Maxfield et al. (1971) conducted one of the earliest investigations of the effects of electric fields on long-term survival. They exposed YOY and yearling rainbow trout to low-frequency PDC and concluded that there was no consistent long-term effect. Several lots of fin-clipped YOY were exposed for 30 s in a homogeneous field of 8-Hz, 40-ms pulses at 1 V_p/cm (water 11–13° C, 143–172 µS/cm; 32% duty cycle). Fin-clipped yearlings were similarly exposed but in a field of 5-Hz, 60-ms pulses at 0.75 V_p/cm (water 9–11° C, 114–132 µS/cm; 30% duty cycle). During exposure, none of the YOY but 4 to 84% of the yearlings were narcotized. All narcotized fish revived immediately and all fish were alive 2 days after treatment. The fish were held with untreated controls of the same age group until maturity. Cumulative mortalities were 9.9% after 3 years for trout exposed as YOY versus 16% for controls and 7.1% after 2 years for those exposed as yearlings versus 10.4% for controls.

Ellis (1974) narcotized age-2 channel catfish with 60 s of DC, 60-Hz AC, or 15, 20, or 25-Hz, exponential-wave PDC at 1.5V/cm and found no significant effect on survival 133 days later. The fish were confined to cages in ponds. Mortality ranged from 0 to 25% among treatment fish and 0 to 23% for controls and was attributed to vegetation-limited exchange of water, predation by snakes, and escape through holes torn in the cage netting by turtles.

Barrett and Grossman (1988) reported no significant differences in delayed mortality for mottled sculpin (3–9 cm SL) collected in late winter by DC electrofishing (600 V, 200 W continuous) and kick seine (0–11% and 0–15% mortality, respectively). Although sample sizes were too small for statistical analyses, they also reported little or no mortality for largescale stoneroller, rosyside dace, warpaint shiner, Tennessee shiner, longnose dace, creek chub, and northern hog sucker. The fish were collected from a North Carolina stream (5–8° C, 10–15 µS/cm) and monitored for 1 month.

Taube (1992) conducted a series of controlled experiments in the slowly flowing water of a hatchery raceway (11° C, 103 µS/cm) with heterogeneous fields of DC, CPS, and four other variations of square-wave PDC, but after monitoring treatment fish, large rainbow trout ($\bar{x}$ = 38–42 cm FL), in a raceway for 128 days, he reported no statistically significant differences in survival despite mortalities of 0% for DC and 8 to 25% for the PDCs (probably due to small sample sizes of 12 fish per treatment). Furthermore, comparing these data to the observation of 10% mortality for control fish not subjected to electric current and maintained in a raceway for another long-term survival experiment (203 days–discussed below), Taube could not attribute any mortality in this experiment to the treatments. For this experiment, trout were individually placed at the distal end of the exposure area and scared or chased towards the electrodes into the effective portion of the field where they were shocked (stunned) for 5 s. Output voltage was 200 V for all treatments except CPS for which voltage had to be doubled to stun fish. Incidence of spinal injury was assessed by X-ray and ranged from 8 to 67%. Most, if not all, mortalities occurred within 21 days.

Schneider (1992) stated that although AC electrofishing was an important technique in fishery management and research, he had not found prior quantitative information about its effects on survival and growth of fish under typical field conditions. Accordingly, he analyzed tag data for largemouth bass and walleye initially captured by 3-phase AC electrofishing, trap netting, or angling in Michigan lakes and ponds during mark-recapture investigations and reported no long-term differences in survival among these capture methods. As noted earlier under "Type of Current," he also found that 3-phase AC electrofishing did not measurably increase the shorter-term mortality (1–33 days) of several species of warmwater and coolwater fishes.

After monitoring adult northern pike (38–77 cm FL) for a month, Roach (1992) detected no significant

differences in mortality among shocked fish with spinal injuries (5%), shocked fish without spinal injuries (9%), and controls (9%). The fish, which were initially collected from South Dakota and Colorado reservoirs by gill net and seine, were exposed to 5 s of homogeneous 120-Hz PDC (50% duty cycle, 4.2 ms pulse width) at 0.14 to 2.21 V_m/cm ($\bar{x}$ = 0.93 V/cm). Treatment fish and controls were tagged, measured, X-rayed, and placed in ponds to monitor survival and growth during the next month. Spinal injuries, mostly misalignments (class 2), were induced in 28% of the treatment fish.

Zeigenfuss (1995) indirectly assessed survival by comparing catch rates among shocked-injured, shocked uninjured, and control rainbow trout stocked in a highly controlled lake fishery in Colorado. Despite observing a lower catch rate for shocked fish in the first of two study years, he reported that differences in survival were not significant for either year. As summarized earlier under "Field Intensity," treatment fish (15–35 cm TL) were shocked for 2 s in homogeneous fields of 60-Hz, square PDC with sufficient intensity to induce spinal injuries, X-rayed to document injuries, measured, and tagged before release in April of two consecutive years. The lake was open to anglers from May through September each year and all fish caught were processed at an exit check station. Captures of control fish were greater than shocked fish in the first year (22% and 17%, respectively) but similar in the second year (15% and 16%, respectively). Most of the difference in capture rates for the first year was due to a lower catch rate of shocked-injured fish. For this reason and because the incidence of spinal injury and mortality within 24 h of treatment was notably greater for shocked fish in the first year than in the second, Zeigenfuss (1995) suggested that although not statistically significant, the observed difference in capture rates that first year was probably due to differential survival.

Dwyer and White (1995) exposed hatchery rainbow trout ($\bar{x}$ = 33 cm TL) to single 10-s exposures of 250-Hz, half-sine PDC and reported 8% mortality within 24 h but no delayed mortality during the next 35 days of the experiment. The fish were individually exposed in a homogeneous field at 3.5 to 3.9 V_p/cm (0.9–1.0 V_m/cm; 8° C, 270–340 µS/cm) and presumably stunned (not specifically stated by the authors). Based on X-rays (and follow-up necropsies when possible injuries were detected), no spinal injuries were detected among fish preserved immediately after treatment, those that subsequently died, or a 40% sample of surviving treatment and control fish 35 days after exposure (hemorrhages and non-spinal injuries were not reported).

Tipping and Gihuly (1996) found that tag returns for adult steelhead (rainbow trout) subjected to electrical anesthesia (29–53%) were consistently 6 to 18% less ($\bar{x}$ = 8%) than for those subjected to carbon-dioxide anesthesia (35–60%), but the differences were significant only for an intermediate electrical treatment (8-s exposures at 1 V_p/cm with returns 18% less than for corresponding fish anesthetized with carbon dioxide). Fish were anesthetized with homogeneous fields of CPS from 0.2 V_p/cm for 100 s to 1.7 V/cm for 3.6 s or carbon dioxide bubbled through a tank at 10 l/min (fish left in the tank until narcotized, usually several minutes). They were then processed, tagged, held for 1 to 2 days, released downstream in the river, and later caught by anglers or at upstream hatcheries. No mortalities were observed prior to release. Although requiring more exposure time to induce sufficient narcosis, electrical treatments using the lowest field intensities (0.2 and 0.3 V_p/cm) produced a less violent response and resulted in the least differences in returns after release (only 6–7% less than fish anesthetized with carbon dioxide). Tipping and Gihuly (1996) concluded that electroanesthesia might be detrimental, possibly due to spinal or related injuries (in preliminary experiments at 1.7 V_p/cm, spinal compression fractures occurred in 8% of exposed fish), but that if it is used as an alternative to chemical anesthesia, injuries and mortalities caused at the lower field intensities might be acceptable.

Although they lacked controls for comparison, Dalbey et al. (1996) implied that 40 to 46% mortality recorded for wild rainbow trout within 335 days after capture by DC, 60-Hz PDC, or a hybrid of the two currents (Fig. 5J) was comparable to expected annual mortality of age-2 and older rainbow trout in Montana rivers and therefore probably not caused by electrofishing. Captured fish were X-rayed to document spinal injuries then maintained for observation in an irrigation pond. Dalbey et al. (1996) found no differences in mortality among currents of capture or relative to presence and severity of spinal injury upon capture.

Kocovsky et al. (1997) investigated the long-term effects of annual electrofishing on stream fish and detected no adverse population effects for brook trout, brown trout, or rainbow trout (populations remained stable or increased), but a notable effect on longnose sucker (population declined significantly in the third year). They conducted three-pass electrofishing with 100-Hz PDC in three streams for a period of 8 years. Incidences of externally detected spinal injuries (mostly cumulative from prior years of electrofishing) were assessed during three of those years and despite lack of negative effect on population size, were found to increase cumulatively. Based on X-rays of over 100 specimens, Kocovsky reported, like many other researchers, that actual incidences of spinal injury were much higher than could be detected externally.

Ruppert (1996) and Ruppert and Muth (1997) reported no significant effect on survival for juveniles of the endangered bonytail 98 days after exposure to

electrofishing currents. They exposed 720 fish (5–8 cm TL) to CPS or 30-, 60-, or 80-Hz PDC at intensities sufficient to induce taxis, narcosis, or tetany. No externally obvious injuries were observed and no vertebral damage was found among the half of each treatment and control group examined for internal injuries, but 13% of the exposed fish suffered spinal hemorrhages.

Unlike most investigations, one study reported by Taube (1992) resulted in significantly greater mortality among fish exposed to an electric field than among controls monitored for 203 days. In addition to an experiment discussed earlier in this section (for which differences in mortality were not significant), Taube (1992) exposed 102 rainbow trout (32–54 cm FL) to 5 s of homogeneous 60-Hz, 50%-duty-cycle PDC at 2.3 V_m/cm (10–12° C, 95–104 µS/cm). Along with 50 control fish, the exposed fish were X-rayed, weighed, measured, and maintained in a raceway to assess long-term survival and growth. Taube (1992) reported 52% mortality for exposed fish that suffered spinal injuries (mostly class 2 injuries, misalignments), 29% for exposed but uninjured (with respect to detectable spinal injuries), and 10% for the controls; 83% of the deaths occurred within the first 30 days.

Based on mark-recapture and radio-tag investigations in the Colorado River Basin, long-term survival of initially electrofished endangered species does not appear to be a serious problem. Many Colorado pikeminnow and smaller numbers of humpback chub and razorback sucker have been electrofished, radiotagged, and subsequently monitored for extended periods (Tyus and McAda, 1984; Wick et al., 1985, 1986; Tyus et al., 1987; Osmundson and Kaeding, 1989; Valdez and Masslich, 1989; Tyus and Karp, 1990). Most survived electrofishing and radio-tag implant surgery and were assumed to behave (move about) normally between and during subsequent contacts. A far greater number of endangered and other fish initially collected by electrofishing were tagged with dangler, anchor, coded-wire, or PIT (passive integrated transponder) tags. Some of these fish have been recaptured one or more times by electrofishing or other means, sometimes several years later (Hawkins, personal communication). The fate of fish that were not recaptured is unknown, but if recaptured fish had incurred electrofishing injuries, the injuries were not externally obvious or not documented.

Effects on Growth and Condition

Even if exposure of fish to electric fields typically has little, if any, affect on long-term survival of fish (most electrofishing mortality is immediate or occurs within a few days), it might impact subsequent growth and condition of at least some species. Results of many, but not all, investigations discussed below suggest that such effects may be significant, especially in the case of multiple exposures over short periods of time and among fish known to have suffered spinal injuries. Accordingly, impacts on growth and condition could be a serious concern for fishery managers and others seeking to safeguard, recover, or enhance aquatic ecosystems.

Most investigations discussed in this section also included a survival component. Refer to corresponding accounts in the preceding section, "Effects on Long-Term Survival," for additional information on nature of the studies and survival results.

Contrary to the results of most investigations discussed below, most early and some more-recent investigations of growth subsequent to electrofishing events or controlled electrical exposure failed to reveal significant adverse effects. According to Halsband (1967), even long treatments with different types of current did not affect the general condition or growth of common carp. In a very long-term study, Maxfield et al. (1971) exposed YOY and yearling rainbow trout to low-frequency PDC, monitored them through maturation, and concluded that there were no consistent effects on subsequent growth. Likewise Ellis (1974) narcotized 2-year-old channel catfish with 60 s of 60-Hz AC, 15- to 25-Hz, exponential-wave PDC, or DC at about 1.5V/cm and found no significant effect on growth 133 days later. Kynard and Lonsdale (1975) held yearling rainbow trout (~12 cm) under DC narcosis for 1, 2, 4, and 6 h (0.25 V/cm, 13–21° C, 450 µS/cm) but reported no mortalities for exposures up to 4 h and no effect on growth 25 days later, even for survivors of 6-h trials (7% short-term mortality). Based on 1- to 2-year mark-recapture tag data, Schneider (1992) reported no significant differences in growth for largemouth bass and walleye initially captured by AC electrofishing, trap netting, or angling in five Michigan lakes and ponds.

In a laboratory experiment, Ruppert (1996) and Ruppert and Muth (1997) reported that long-term (98-d) growth in juvenile bonytail (an endangered species) was not significantly affected by exposure to any of several electrofishing currents or levels of intensity. After 49 days, mean weights increased 24 to 39% for treatment fish and 26 to 27% for controls; after 98 days, mean weights had increased by 42 to 54% and 42 to 44%, respectively. Based on necropsy of half of the treatment and control fish, they found that 13% of the shocked fish (range 3–27% among treatments) had spinal hemorrhages but no obvious damage to the vertebrae. They cautioned readers that significant negative effects on growth due to these injuries might be more likely to occur in a dynamic riverine ecosystem than under laboratory culture.

Among investigations reporting significant effects of electrical exposure on growth, Dwyer and White (1995) reported significantly less growth for shocked adult rainbow trout (9% less in TL, 34% in g) and yearling Arctic grayling (15% in TL, 23% in g) during 35 and 28-day

monitoring periods, respectively, after exposure than for controls. In contrast, both shocked and control yearling cutthroat trout experienced very little increase in length during the 28-day monitoring period, with no significant difference between them, and actually lost weight, with shocked fish losing significantly more than controls. The rainbow trout (initially $\bar{x}$ = 33 cm TL) were subjected to 10 s of 250-Hz PDC (8° C, 270–340 µS/cm) and the Arctic grayling and cutthroat trout (12–18 cm TL) to 10 s of 500-Hz PDC (9.6° C). X-rays of 44 exposed rainbow trout revealed no spinal trauma (20 frozen immediately after treatment, 4 upon death within 24 h, and 20 of 50 monitored for 35 days); the yearling fish were not X-rayed for spinal injuries.

In a field investigation, Thompson (1995) and Thompson et al. (1997b) assessed the effects of electrofishing on growth and body condition of brown trout and rainbow trout (>18 cm TL) 1 year after initial capture and concluded that annual electrofishing had some adverse effects on fish growth or condition, but not consistently. Fish in three Colorado rivers were captured using 60-Hz, half-sine PDC with a mobile (throwable) anode and marked with visible implant tags. Recaptured fish were compared to control fish not captured the year before and assumed to not have been shocked in that previous year (authors recognized that some fish might have been exposed but either escaped the electric field or capture). Growth was based on back-calculations for the last-annual increment of scales and validated for tagged fish by comparison with differences in length since initial capture. Unreadable scales or failure to validate back calculations reduced sample size such that only four species-river-age comparisons were statistically valid. In one river, age 4 and 5 unshocked brown trout grew significantly more than shocked brown trout. Likewise for age-5 rainbow trout in another river. Although the mean growth increment for previously shocked fish also was less than for controls in the remaining two valid comparisons, the differences were not statistically significant. In one river-year comparison, average condition factors were significantly higher for unshocked brown trout (22–36 cm TL) and rainbow trout (32–41 cm TL) than for previously shocked fish–average weights were 11% and 9% greater, respectively. In eight other species-river-year comparisons, condition factors were not significantly different. Based on other investigations, Thompson et al. (1997b) suggested that differences they observed in growth and condition may have been caused by electrofishing injuries.

Acknowledging earlier reports of no significant impact on growth after single electrical exposures, Gatz et al. (1986), noted that several short-term physiological effects had been identified by Horak and Klein (1967), Schreck et al. (1976), Bouck et al. (1978), and Burns and Lantz (1978), and hypothesized that repetition of these physiological effects through repeated electrofishing, as in multiple-capture studies, might measurably affect subsequent growth. In a field study carried out for 1 year in very low-conductivity streams in Tennessee and North Carolina (5–10 µS/cm, salt blocks were necessary to increase conductivity), Gatz et al. (1986) monitored the individual growth of rainbow trout and brown trout of various ages that were electrofished with 600-V, 120-Hz PDC twice within a 1 to 3-day period repeatedly at intervals of 1.5 to 7 months. They reported that significant numbers of fish lost weight, in both the short term (1–3 days, 81% lost an average of 5% of their body weight) and long term (48% of the fish electrofished within 3-month intervals). The percentage of fish with instantaneous growth rates less than average was significantly greater for fish that were electrofished four or more times during the year, at intervals of less than 3 months, or at a young age (ages 1 and 2). Gatz et al. (1986) concluded that "studies should be designed to avoid repeated electroshocking, especially at intervals of less than 3 months." They also suggested that "growth studies in which more than a small fraction (e.g., >20%) of the total population is repeatedly electroshocked at short (<3 month) intervals are likely to underestimate growth rates." Although no external signs of injury were noted, Gatz et al. (1986) mentioned tissue damage which might require up to 3 months for complete recovery as a possible explanation. Fish were not examined by X-rays or necropsy to confirm this suspicion.

Based on a laboratory experiment, Gatz and Adams (1987) also concluded that time intervals between repeated electrofishing should be maximized to limit impacts on growth. They exposed hybrid bluegill x green sunfish to 400-V, 120-Hz PDC once a week for 3 months and found that growth was about 37% less than for controls and 29% less than for fish exposed only once or at 2 or 4 week intervals (differences between the latter two groups were not significant).

Dwyer and White (1997) followed their single-exposure PDC short-term growth experiments on juvenile Arctic grayling and cutthroat trout (Dwyer and White, 1995, discussed above) with a longer-term, multiple-exposure investigation and reported significant effects varying with species and electrical current, intensity, and exposure. Using juvenile Arctic grayling (15–25 cm TL, 29–121 g) and Yellowstone cutthroat trout (12–17 cm TL, 14–41 g) and the same homogeneous field exposure tank as in the earlier experiments (390 µS/cm, 7° C), they compared the long-term effects on growth of two 5- or 10-s exposures, 10 to 14 days apart, in smooth DC or 60-Hz, square-wave PDC at 0.75 V_p/cm (lower intensity; 25% duty cycle for PDC) and 1.5 V_p/cm (higher intensity field; 33% duty cycle for PDC). For Arctic grayling 100 days

after initial treatment relative to controls, they reported: (1) no significant difference in growth for fish exposed to 5 or 10 s of low-intensity DC; (2) significantly less growth in length (22–29% less) but not weight for fish exposed to 5 or 10 s of high-intensity DC; and (3) significantly less growth in length (56–71% less) and weight (63–76% less) for fish exposed to 5 or 10 s of low or high-intensity PDC. For the cutthroat trout relative to controls, they reported: (1) no significant difference in growth for fish exposed to 5 or 10 s of high-intensity DC or 5 s of high-intensity PDC, (2) significantly less growth in length but not weight for fish exposed to 5 s of low-intensity PDC (19% less) or 10 s of low-intensity DC (15% less), and (3) significantly less growth in length and weight for fish exposed to 5 s of low-intensity DC (12% less in TL, 10% in g) or 10 s of low or high-intensity PDC (25–27% less in TL and g). Some of the significant differences for cutthroat trout appear counter-intuitive and all are much lower in magnitude than for Arctic grayling. Based on results for both species, the authors concluded that smooth DC was less harmful. Although not as strongly supported by their results, they also recommended lower voltages and shorter exposures to minimize potential long-term effects on growth.

Although initially much smaller in size, control and treatment juvenile cutthroat trout in the above experiments (Dwyer and White, 1997) grew nearly 50% more in length and 25% more in weight in 100 days than Arctic grayling. In contrast, growth after 28 days for juvenile cutthroat trout in their single-exposure experiment (Dwyer and White, 1995; discussed above) was almost nil, but PDC frequency and peak field intensity were much higher.

Because of problems in objectively assessing the degree and impact of electrofishing injuries on a fishery, Holmes et al. (1990) recommended assessing effects at the population level by testing for differential survival and growth over time between fish with electrically induced spinal injuries and control groups. Three such investigations have been conducted with mixed results.

Unlike the significant mortality reported by Taube (1992) for injured rainbow trout ($\bar{x}$ = 39 cm FL; mostly spinal misalignments) during a 203-day monitoring period after exposure to 5 s of homogeneous 60-Hz PDC at 2.3 V/cm (most mortality within the first 30 days; see discussion above under "Effects on Long-term Survival"), he found no significant differences in growth among exposed-injured, exposed-uninjured, and control trout. Mean increases in length were 29, 42, and 37 mm, respectively, and corresponding mean increases in weight were 320, 381, and 355 g. However, results were compromised by small sample sizes due to lost tags, especially for injured fish. Taube suggested that differences might be significant in a wild population where injury could affect ability to capture prey.

In the first, but not second, of two annual trials, Zeigenfuss (1995) found that average daily growth rate among captured rainbow trout (15–35 cm TL) stocked in a highly controlled Colorado lake was significantly lower for shocked fish with spinal injuries than for either controls or shocked-uninjured fish (no significant difference between the latter two groups). Most of that overall difference occurred among fish measuring 29 to 32 cm TL. No significant differences in growth rates were detected for any size groups during the second-year trial. Differences in results between years might be explained, at least in part, by the greater incidence of spinal injury observed among electrically exposed trout during the first year.

Dalbey et al. (1996, also Dalbey, 1994) compared changes in length, weight, and condition factor for wild rainbow trout 335 days after capture by DC, 60-Hz PDC, or a hybrid of the two currents (Fig. 5J) and reported significant differences in growth relative to both electrofishing current and presence and severity of electrofishing injury upon capture. Captured fish were X-rayed to detect spinal injuries, then maintained for long-term observation in an irrigation pond. Among trout captured by the different currents, growth did not differ significantly 100 days later but it was significantly greater for the hybrid current than for DC or 60-Hz PDC at 335 days (respectively, 112% and 51% greater for mean increase in length and 79% and 58% greater for mean increase in weight). There were no significant differences in mean condition factors relative to electrofishing current. Combining data for all currents, uninjured fish grew significantly more through the first 100 days than fish with spinal injuries (~1.5 times more in mean length and 16 times more in mean weight). By 335 days, uninjured fish and those suffering only vertebral compression fractures (class 1) grew significantly more than fish with more severe (class 2 and 3) spinal injuries (>3 times more in both mean length and mean weight). Fish with the most severe spinal injuries (class 3) actually lost mean weight. Condition factor declined for all groups by 100 days after exposure, but the decline was significantly greater for injured fish. By 335 days, condition factors increased beyond that at capture for all groups except the most severely injured fish and was significantly greater for uninjured than for injured trout. Dalbey et al. (1996) concluded that the negative effects of electrofishing injury on growth and condition are likely to persist for at least a year after injury and speculated that in a dynamic stream environment, spinal injuries could have even greater negative effects.

Among recaptured endangered and other native cypriniform fishes that were initially captured by electrofishing, tagged, and subsequently recaptured one

or more times in the Upper Colorado River Basin (see last paragraph under "Effects on Long-term Survival"), Bestgen et al. (1987) and Hawkins (personal communication) found some fish that had grown very little in length, not at all, or even lost length between captures, even a year or more after the initial or prior capture. Spinal injuries, including compressed vertebrae, or long-term physiological stress might account for at least some of these poor or no growth observations.

Effects on Reproduction and Gametes

Spawning or near-ripe fish often aggregate in accessible localities and are sometimes considered more vulnerable to electrofishing than at other times of the year (Stewart, 1967, as cited by Lamarque, 1990; Kolz and Reynolds, 1990b). For these reasons, some fish are targeted for collection by electrofishing during the spawning season. Also, broodstock for experimental or hatchery culture are often collected by electrofishing or subjected to electronarcosis prior to hormone injection or extraction of gametes for artificial fertilization of eggs. If fish in spawning condition are particularly susceptible to electrofishing injury or there are significant adverse effects of these practices on spawning behavior or gametes, the impacts might in turn affect hatchery operations or natural reproduction, a matter of particular concern for small isolated populations or endangered species.

Most knowledge of the effects of electric fields on fish reproduction and gametes is based on collection of broodstock, hatchery operations, and survival of artificially fertilized eggs. Unfortunately, conclusions drawn from these observations and experiments are mixed but sufficient to warrant caution, ongoing scrutiny, and perhaps reevaluation of the practices.

Several investigators have reported evidence of no harmful effects of electrofishing or electroanesthetizing broodstock on the viability of artificially fertilized eggs and recently hatched offspring. Halsband (1967) reported that gonads were not harmed by electrofishing, and Halsband and Halsband (1975, 1984) stated that "Harmful genetic effects–or harmful effects to the progeny–are also not produced." According to Vibert (1967b), "McGrath reported that . . . no ill effects have been recorded in hatcheries on the offspring of wild trout caught by electricity." Maxfield et al. (1971), who subjected YOY and yearling rainbow trout to 8-Hz and 5-Hz PDC, respectively, and documented the lack of effects on long-term survival and growth (see discussions in corresponding sections above), also reported that subsequent fecundity of those fish and mortality of their offspring through eyed-egg, hatching, and initial feeding stages were not consistently different from those of unexposed fish. Khakimullin and Parfenova (1981) reported no ill effects of pulsed 6-Hz, 40-ms AC (probably PDC from rectified AC) on Siberian sturgeon spawners or subsequent (pituitary-induced) gamete maturation and development of eggs and larvae. Similarly Valdez (personal communication) and Pfeifer (personal communication) reported no adverse effects of PDC electrofishing on ripe lake trout and walleye, respectively, or on the survival of their artificially fertilized eggs. Even when broodstock are injured by exposure to electricity, eggs may not be adversely affected. Tipping and Gihuly (1996) reported that in one instance, ripe eggs were successfully extracted from a few coho salmon that had apparently suffered spinal injury and swam upside down for more than 2 weeks.

Walker et al. (1994) found that survival of fertilized northern pike eggs through an eyed stage was nearly the same whether broodstock was electrically (10 s of 50-Hz, 7.6-ms, PDC at 0.6 V/cm) or chemically (tricaine methanesulfonate = MS-222) anesthetized (55% vs. 56%). Ripe broodstock (45–97 cm SL) for this comparison were collected from the Mississippi River by frame nets, anesthetized, and stripped of eggs and milt for hatchery propagation. All electrically anesthetized fish were swimming upright within 3 min and none of the fish died or showed external signs of injury within 24 h of electrical exposure.

Tipping and Gihuly (1996) reported that mortality of chinook salmon eggs and larvae through swim-up was significantly greater for those reared from unshocked broodstock (mean 12%, range 6–19%) than from electrically anesthetized fish (means 6–7%, range 4–8%). The latter were subjected to 18 s of CPS at 0.4 V_p/cm or 4 s of CPS at an estimated 1.4 V_p/cm immediately prior to being killed for collection of eggs and milt. There was no significant difference in egg and larval mortality relative to electro-anesthetic protocols. For all treatment and control groups, most mortality occurred by the eyed-egg stage.

In contrast to discussion above, Marriott (1973) and other investigators have documented significantly greater mortality for the progeny of captive or wild broodstock that were subjected to electric fields prior to spawning or extraction of gametes. Marriott (1973) compared mortality of artificially fertilized pink salmon eggs from unshocked and electrocuted (110-V, 60-Hz AC) males and females. He found mortality through a late-eyed stage to be 12% higher for eggs from electrocuted females. Two electrocuted females had severely ruptured internal organs, and most of their eggs were loose and bathed in body fluids that might have accounted for at least some subsequent egg mortality. Additional exposure of a batch of fertilized eggs from electrocuted adults to an electric field resulted in an additional 15% mortality, 27% greater

mortality than for eggs never exposed to an electric field. Marriott (1973) recommended that electrofishing not be used to capture ripe females.

Newman and Stone (unpublished manuscript, 1992) subjected ripe walleye to 120-Hz, quarter-sine PDC (400 V), stripped and artificially fertilized the eggs, and documented significantly greater mortality for these embryos (63–65%) than for embryos from controls ($\bar{x}$ = 37%). Broodstock were exposed in a net enclosure as an electrofishing boat made two slow passes about 0.7 m from the net.

Newman and Stone (unpublished manuscript, 1992) also reported that the manager of the Lac du Flambeau Tribal Hatchery had severe viability problems with eggs from electrofished brown trout. He and other hatchery managers observed broken eggs when stripping electrofished brown trout and suspected that albumen from the eggs might have clogged the micropyles in many unfertilized eggs. According to Newman and Stone (unpublished manuscript, 1992), some biologists also suspect that electrofishing might cause a loss of sperm motility in ripe males, but experimental confirmation of such has not been published.

Roach (1996) monitored the fertilized eggs from wild broodstock of four salmonids captured by electrofishing and reported significantly greater mortality than for eggs from controls. Using 60-Hz, square-wave, PDC (50% duty cycle), he electrofished chinook salmon (63–98 cm FL; 145 μS/cm; 11° C), least cisco (29–41 cm FL; 138 μS/cm; 7° C), and humpback whitefish (37–48 cm FL; 138 μS/cm; 7° C) and exposed weir-trapped Arctic grayling (25–38 cm FL) in a net pen (340 μS/cm; 5° C). Arctic grayling and chinook salmon were exposed to mean field intensities up to 1.4 and 1.2 V/cm, respectively, at 2.5 cm from the anode. All fish were netted while in a state of narcosis. Eggs from these fish and corresponding controls caught by other means were stripped, fertilized, incubated, and monitored up to the eyed stage. Eggs were collected on the day of exposure for all but chinook salmon which were stripped 3 days after exposure. Mortality up to the eyed-stage for embryos from shocked versus unshocked parents was 4% vs. 2% for Arctic grayling, 20% vs. 1% for chinook salmon, and 57% vs. 52% for least cisco; mortality for humpback whitefish was 41% but controls were not available for comparison). The difference in mortality figures was greatest for chinook salmon (19%), perhaps because its eggs were collected 3 days after exposure rather than on the same day.

Muth and Ruppert (1996) subjected ripe broodstock of endangered razorback sucker to electrofishing fields and reported injuries to the adults, premature expulsion of gametes, and significantly greater mortality of progeny through hatching than for controls. Captive ripe males (50–55 cm TL) and near-ripe females (55–60 cm TL) were transported from a national hatchery and the females injected with hormone to induce ovulation. Treatment fish (2 replicates, each with 2 males and usually 2 females) were exposed to 10 s of either CPS or 60-Hz, 4-ms, square-wave PDC, each at a homogeneous intensity of 1 V_p/cm (610 μS/cm; 20° C). Tetany was induced in all fish but was incomplete for those exposed to CPS (fish continued to quiver). All fish expelled gametes during treatment, at least several hundred eggs per female. No external hemorrhages were observed but subsequent necropsy and X-ray analysis revealed spinal injuries or associated internal hemorrhages in 50% of the fish exposed to 60-Hz PDC and 14% of those exposed to CPS (see earlier discussion under "Pulse Trains"). No spinal injuries or hemorrhages were detected in control fish and no damage to internal organs was observed for either treatment or control fish. Fertilized eggs were divided into lots of 500, five for each treatment replicate and ten for controls, incubated at 18° C, and checked twice daily for removal of dead eggs until hatching. About 8 to 12% of samples of treatment and control eggs preserved prior to fertilization had ruptured chorions. Mortality through hatching for controls, 65 to 79% ($\bar{x}$ = 74%), was quite high but within the range reported by hatcheries for razorback sucker (45–77%). Mortalities for 60-Hz PDC and CPS treatments were significantly higher at 83 to 96% ($\bar{x}$ = 89%) and 90 to 98% ($\bar{x}$ = 95%), respectively, but the difference between the two treatments was not significant. Muth and Ruppert (1996) recommended that the practice of electrofishing spawning aggregations of endangered razorback sucker be carefully reevaluated.

In the only investigation of effects of electrofishing ripe or near-ripe fish on natural reproductive behavior, Sorensen (1994) concluded no long-term consequences. He subjected spawning goldfish (32 females and 24 males; spawning induced by injection of prostagladin F2 in females) to 15 s of 100-Hz, square-wave PDC in an aquarium. Recovery times were greater than 10 min, but no short-term mortality or brands were reported. Twenty-four hours after being stunned, females were again injected and the fish spawned normally. In a field investigation, Sorensen exposed naturally spawning brook trout (11 males and 9 females) to 30 s of rippled DC in a Minnesota stream. After recovery, all fish were released back into the stream in good condition and nearly half (5 males and 3 females) were observed to spawn.

Effects on Early Life Stages

Electric fields are of no value in the collection of already spawned fish eggs, and few biologists have applied electrofishing technology to the collection of fish larvae and early juveniles (Snyder, 1983; Copp, 1989; Kelso and Rutherford, 1996). Accordingly, most concern about

harmful effects on fish eggs and larvae pertains to their incidental exposure during electrofishing operations for larger fish. Although based on very few investigations and limited primarily to salmonids, Lamarque (1990) noted that evidence to that date suggested that embryos are particularly sensitive between fertilization and eyed-egg stages and recommended that electrofishing over active spawning grounds should be avoided.

Godfrey (1957) determined that mortality in brook trout and Atlantic salmon embryos was low when exposed to electric fields during the first few hours (water hardening; precleavage stages), high when exposed at some point thereafter until the eyed-egg stage, then low again when exposed anytime during the remainder of embryonic development. As discussed below, more recent investigations on other species have generally substantiated Godfrey's (1957) observations, and one, as surmised by Kolz and Reynolds (1990b), suggested that this pattern of greater sensitivity to electricity before the eyed-egg stage is similar to that for mechanical shock.

Dwyer et al. (1993; also Dwyer and Fredenberg, 1991) found that for rainbow trout embryos reared at 10° C, cumulative mortality to day 26 or 27 (just a day or two before hatching) followed a nearly normal distribution relative to age at exposure (2 to 26 days) for both electrical and mechanical shock with peaks on day 8 (10 days before eye up and 20 days before hatching). Mortalities for embryos treated at this most sensitive time (day 8) averaged 99% for eggs dropped 15 cm from one container to another, 58% for eggs exposed to 10 s of homogeneous 250-Hz PDC at about 3.4–3.8 V_p/cm (0.9–1.0 V_m/cm, 270–340 μS/cm, 8° C), 30% for those handled but not shocked, and about 20% for unhandled controls.

Noting that walleye have a much shorter incubation period than rainbow trout and that peak sensitivity to mechanical shock for walleye embryos occurs at about 24 h after fertilization, Newman and Stone (unpublished manuscript, 1992) found that walleye embryos also were more sensitive to 120-Hz, quarter-sine PDC (400-V, 3-A output) when exposed at 24 h than 48 h of age. For their experiment, eggs were placed in nylon mesh bags and laid on a lake bottom over typical walleye spawning substrate then exposed to a single pass of current from an electrofishing boat. The difference in average mortality between embryos exposed at 24 h and controls was 19% (64% vs. 45%), whereas the difference between those exposed at 48 h and their respective controls averaged only 3% (56% vs. 53%).

Embryos also may be detrimentally irritated by electric fields near the end of the embryonic period. Luczynski and Kolman (1987) used AC to induce premature hatching in powan embryos.

The impact of electrical factors such as duration of exposure, field intensity, and type and waveform of current on embryos has been investigated by several researchers. As early as the beginning of the 1920's, Scheminzky (1922, according to Lamarque, 1990), subjected trout eggs to long exposures in a DC field and reported movements of embryos and one incident of high mortality. Although exposures in Scheminzky's (1922) experiments were far longer than those likely in normal electrofishing operations (Lamarque, 1990), perhaps they were not so different from what drifting eggs or larvae (e.g., freshwater drum, emerald shiner, striped bass) might experience near electric screens or barriers.

In addition to determining the most sensitive stages during embryonic development, as discussed above, both Godfrey (1957) and Dwyer et al. (1993; also Dwyer and Fredenberg, 1991) found that mortality during these stages increased with both field intensity and exposure time. In Dwyer et al.'s (1993) investigation, 8-day-old cutthroat trout embryos were exposed to 5, 10, or 20 s of homogeneous CPS at 2.4, 3.8, 5.3, and 6.7 V_p/cm and assessed for mortality 10 days later (about eyed-egg stage). Combining exposure times, mortality increased with field intensity from less than 15% for controls and treatments at 2.4 V_p/cm to 20 to 45% at about 3.8 V_p/cm, 85 to 100% at about 5.3 V/cm, and approximately 100% at 6.7 V_p/cm. For embryos subjected to 3.8 V_p/cm, they reported significant increases in mortality with exposure duration from approximately 20% for 5-s to 30% for 10-s and 42% for 20-s exposures.

Furthermore, Dwyer and Erdahl (1992, 1995) found that field intensity had greater impact on mortality of cutthroat trout embryos than either current type or PDC pulse frequency. They exposed separate batches of 2- to 18-day-old embryos every second day to 10 s of homogeneous DC at 1.4 and 2.2 V_p/cm, 30- or 60-Hz, square-wave PDC (50% duty cycle) at 1.4 and 2.2 V/cm (probably peak–if mean, corresponding peak voltage gradients would be 2.8 and 4.4 V/cm), or CPS at 3.4 and 4.3 V_p/cm; 10-day-old embryos were exposed also to CPS at 1.4 and 2.4 V_p/cm (7.8° C, 388 μS/cm; voltage gradients calculated). Mortalities for all treatments were assessed on day 18 (eyed embryos). Mean mortalities for controls ranged from 3 to 11% and was greatest for 12-day-old embryos. Mean mortalities were similar to controls for all treatments at 1.4 V/cm except DC on days 8, 10 and 12 (19, 22 and 29%, respectively), all treatments on day 2 except DC at 2.2 V/cm (47%) and CPS at 3.4 V/cm (52%, no data for 4.3 V/cm), and, as in investigations by Dwyer et al. (1993) and Roach (1996, discussed below), for all treatments beyond day 14 regardless of field intensity. The greatest mortalities were observed at the highest intensity levels for DC (2.2 V_p/cm; 84–99% for exposures on days 8–14; no data for days 4 and 6) and CPS (4.3 V_p/cm; 81–99% for days 4–12). Mean mortalities for 30- and 60-Hz PDC treatments at 2.2 V/cm and CPS at 3.4 V/cm on days 6 through 12 ranged

from 22 to 76%. Unlike comparable experiments by Dwyer et al. (1993) and Roach (1996, discussed below) using PDC, mortalities for 30- and 60-Hz PDC at 2.2 V/cm peaked on days 6 and 12 (61–76%) with notably lower mortality between on days 8 and 10 (22–32%). Among current types tested at comparable field intensities, cutthroat trout embryos were at times more sensitive to DC than PDC or CPS. There were no consistent differences in mean mortality between 30- and 60-Hz PDC at comparable field intensities.

Roach (1996), who conducted similar experiments with Arctic grayling and chinook salmon, also reported significantly greater mortality for embryos exposed to electric fields through the eyed-egg stage and that mortality during the more sensitive stages generally increased with increasing field intensity, but he also found a strong species effect and that mortality was usually greater for embryos from recently shocked parents than unshocked parents. Roach (1996) exposed embryos from shocked or unshocked broodstock to 5 s of homogeneous 60-Hz PDC (50% duty cycle) at high (1.3–1.5 V_m/cm), medium (0.8–1.0 V/cm), low (0.3–0.5 V/cm; Arctic grayling only), or no field intensity. Batches were treated once at difference ages, every second or third day from fertilization to or beyond acquisition of dark eye pigment. Mortality rates for exposed embryos were much lower for Arctic grayling (<12%) than for chinook salmon (100%) and peak sensitivity occurred notably later in development (day 10 vs. day 6 for chinook salmon).

For exposed Arctic grayling, Roach (1996) reported that mean mortality rates increased with age at exposure from a low for 2-day-old morulas to a peak for 10-day embryos (~2 days after optic vesicles appeared and 2 days before the eyes became faintly pigmented), then decreased for embryos exposed at later stages. Mortalities for high-intensity treatments of embryos from shocked parents ranged from 7% for day 2 exposures to 12% for day 10 exposures versus 2 to 4%, respectively for controls from unshocked parents. Significant differences in mean mortality included: (1) shocked embryos from shocked parents (6%) versus shocked embryos from unshocked parents (4%); (2) all combinations of embryos shocked by level of field intensity (7% for high, 6% for medium, 4% for low, and 3% for none); (3) embryos shocked at 2 days (4%) versus all other stages (5–7%); and (4) embryos shocked at 10 days versus all other stages (mean percentages not reported).

For chinook salmon, Roach (1996) reported that greatest mean mortality rates were about 90 to 100% for embryos exposed to high field intensity at any stage between morula and early epiboly (3–12 days), regardless of whether parents had been shocked or not. This was comparable to the high mortality Dwyer and Erdahl (1995) reported for 4 to 12-day-old cutthroat trout exposed to high-intensity CPS. For chinook salmon embryos treated at high intensity on day 14 (optic vesicles visible and brain lobes differentiated) or later, mortality dropped sharply to 32 to 42% for those from shocked parents and 2 to 8% for those from unshocked parents. At medium field intensity, response was more like previously discussed experiments with sensitivity increasing progressively to an early peak of 75 to 78% mortality for treatments on day 6 (gastrula stage), again regardless of whether parents were shocked or not. For later-stage treatments at medium field intensity, mortality dropped regressively by the day 14 treatment to 22 to 32% for embryos from shocked parents and 1 to 2% for those from unshocked parents. Mean mortality for corresponding controls was consistently 16 to 24% and 1 to 3%, respectively.

In experiments similar to those by Dwyer and Erdahl (1995) on cutthroat trout embryos (discussed above), Muth and Ruppert (1997; also Ruppert and Muth, 1995, Ruppert, 1996) investigated the harmful effects of electric-field intensity and PDC pulse frequency and pattern on embryos of the endangered razorback sucker and determined that moderately early embryos were most sensitive, mortality following exposure at this early stage was significantly greater for all fields tested, and the highest intensity and highest frequency simple PDC fields tested were most harmful. Embryos at 33 h (early epiboly), 78 h (early tail bud), or 122 h (finfold) postfertilization were exposed for 10 s in one of six homogeneous fields (19° C, 650 μS/cm): CPS or 30-Hz (4-ms, 12% duty cycle), 60-Hz (4-ms, 24% duty cycle), or 80-Hz (5-ms, 40% duty cycle), square-wave PDC at 1.2 V_p/cm; or 60-Hz PDC at 5 or 10 V_p/cm. Mortalities from all treatments through hatching (between 128 and 140 h after fertilization), except for 78-h and 122-h embryos exposed to CPS and 30-Hz PDC, ranged from 22 to 97% and were significantly greater than corresponding controls (5–12%). As for most investigations discussed above, sensitivity to all electric fields was greatest for embryos in a moderately early stage of development (33-h) and decreased significantly with age at exposure except between 78-h and 122-h for CPS and 30-Hz PDC treatments. At 1.2 V_p/cm, differences in mean mortality between treatment and control lots ranged from 38 to 85% for embryos treated at 33 h, 27 to 49% at 78 h (excluding insignificant differences of 2% for CPS and 17% for 30-Hz PDC), and 17 to 25% at 122 h (excluding insignificant differences of 3% for CPS and 5% for 30-Hz PDC). For 78-h and 122-h embryos treated to 1.2-V_p/cm of 30-, 60-, or 80-Hz PDC, mortality increased with increasing pulse frequency but only differences between the 30-Hz and 80-Hz treatments were significant. Mean mortalities for all 33-h treatments were similar at 50 to 60% except for the most intense (10 V_p/cm) 60-Hz PDC treatment which suffered 97% mortality. Among all 60-Hz PDC treatments,

mortality increased with increasing field intensity but the differences were only significant for the most intense treatments with 33-h and 78-h embryos. No notable external morphological anomalies were observed for any larvae that hatched from these treatments. Muth and Ruppert (1997) concluded that electrofishing adult razorback sucker over active spawning grounds could significantly reduce survival of embryos present in or on the substrate.

Muth and Ruppert (1997) also subjected recently hatched, 36-h-old razorback sucker larvae (9.4–9.7 mm SL; ~96 h before swimup) to the same treatments discussed above for embryos and reported a significant reduction in growth during the next 4 weeks, regardless of electrical treatment, but no significant effect on survival. Larvae were immediately tetanized upon exposure to 60-Hz PDC at the higher field intensities (5 and 10 V_p/cm), but during all 1.2 V_p/cm treatments they severely twitched and rapidly swam in random directions. Larvae subjected to 30-Hz PDC and CPS recovered almost immediately after being shocked whereas those subjected to other treatments remained on the bottom of nylon-mesh treatment baskets for several seconds after current was switched off. No fish died within 48 h of treatment and no behavioral anomalies were observed during the 4-week monitoring period after exposure during which survival and growth were assessed at 7-day intervals. Mortality through day 28 averaged 8% for controls and 5% (30-Hz PDC, 1.2 V/cm) to 15% (60-Hz PDC, 1.2 V/cm) for exposed larvae. Growth for all treatment larvae 4 weeks after exposure averaged 0.07 to 0.09 mm/d and was significantly less (31–46%) than the average growth rate of 0.13 mm/d for controls. However, in most cases, significant differences in growth were not detected until 21 days after treatment. There were no significant differences in growth among treatments. The authors discussed the probability that reduced growth rates could significantly affect already limited first-year survival by prolonging vulnerability to starvation and predation.

Based on a limited experiment with precleavage Atlantic salmon eggs buried under about 20 cm of gravel and exposed to DC for about 2 min, Godfrey (1957) concluded that eggs in gravel redds received some protection from shock (mortality 10% vs. 81% for unburied eggs), but such protection was not substantiated in other investigations. In a similar experiment, Dwyer et al. (1993) subjected 8-day-old cutthroat trout eggs in Vibert boxes buried 15 cm deep in several artificial redds to 10 s of 250- or 500-Hz PDC or CPS at voltage gradients of 0.9 to 1.0 V_m/cm. Voltage gradient appeared to be negatively affected by gravel depth when using 250-Hz PDC but not 500-Hz PDC (not mentioned for CPS). Still, cumulative mortalities 10 days after exposure were 95% for CPS, 68% for 250- or 500-Hz PDC, and 56% for controls. The high mortality for the controls and a portion of each shocked group was attributed to sedimentation in redds. Based on these results, other experiments noted above, and measurement of voltage gradients of about 1 V_m/cm at 20-cm depths in artificial redds, Dwyer et al. (1993) concluded that electrofishing in streams where trout have recently spawned can adversely affect egg survival. Roach (1996) also determined that burial in gravel offered little protection to eggs other than as a physical barrier keeping electrodes dragged over the surface at least burial depth away from the eggs. He reported that with an electrode at the surface of a gravel substrate, the drop in voltage gradient with depth in gravel was nearly the same as in water alone (70–72% drop over 40 cm in his experiments). However, he also reported that drop in field strength within the first 10 cm of substrate depth was greater for larger size gravel and cobble than for silt or gravel and silt.

Among the few biologists who used electric fields to capture larvae, Braem and Ebel (1961) used electrified dip nets and McLain and Dahl (1968) an electrified net sled (beam trawl) to capture lamprey ammocoetes, Maty et al. (1986) used electric fields to capture Atlantic salmon larvae after emergence from redds, and Noble (1970) used an electric grid in front of a Miller high-speed sampler to improve the catch of larger larvae and juveniles. Noble (1970) found that the latter electrified sampler had little effect on the catch rate of small larvae. However, because small fish larvae are much less likely to evade the sampler than larger larvae or early juveniles, catch rates of the former might not be expected to differ even if the field was effective.

Perhaps the greatest proponent for use of an electrofishing technique for capture of larvae and small juveniles is G. H. Copp of France. Copp and associates (Copp and Penaz, 1988; Copp, 1989, 1990; Persat and Copp, 1990) used the same portable PDC electrofishing gear that was used locally to capture larger fish but reduced the size of the anode to a 10-cm ring and increased the size of the cathode. This intensified the field within 30 cm or less of the anode sufficiently to induce taxis or narcosis (possibly tetany) in most fish as small as 5 mm SL. The anode, mounted on a 2.5-m handle, was dipped into the water as the deadman switch on the handle was closed for a second or two, then a fine mesh dip net was immediately thrust under the anode to collect the fish. The advantage of this technique over simply using dip nets or hand seines to collect larval and early juvenile fish was samples with a relatively unbiased size range. Usually for larger juvenile and adult fish, both electrodes should be as large as practical to reduce the zone of tetany and maximize the effective size of the field. However, Copp and his associates (Copp and Penaz, 1988; Copp, 1989, 1990; Persat and Copp, 1990) effectively used their very limited range for smaller fish to advantage by combining

the technique with a sampling strategy that consisted of numerous, small, randomly distributed, microhabitat samples (point abundance sampling). The matter of electrofishing injuries and mortality with this method was not a serious concern because sample size was usually small and the collected fish were killed, fixed, and preserved for subsequent processing.

The effects of electrofishing on early life stages appear to vary with species and size. Godfrey (1957) observed that newly hatched Atlantic salmon exhibited increased swimming movement but not taxis in response to a DC field. Maxfield et al. (1971) noted that 30-s exposures to homogeneous, low-frequency PDC fields of 1 V_p/cm failed to induce narcosis in 5-cm YOY rainbow trout, whereas exposures to similar fields at only 0.75 V_p/cm were sufficient to induce narcosis in at least some 19-cm yearlings. Among harmful effects, Lamarque (1990) noted that mortality was common for larval zander but rare for trout larvae; also, salmon parr did not suffer unduly in fields that killed larger smolts. Lamarque (1990) suggested that electric fields that are dangerous to adult fish are probably dangerous to juveniles as well, but because fish larvae and early juveniles are extremely fragile, mortality due to handling and the stress of capture might be as great as that due to electrofishing fields. The occurrence and significance of physical electrofishing injuries to fish larvae and early juveniles was not documented in literature reviewed for this report.

Results — Summary of Survey Responses

A questionnaire to assess local observations and recommendations with respect to electrofishing was distributed directly, or through endangered-species program leaders, to fishery biologists with electrofishing experience in the Colorado River Basin and to fishery faculty and graduate students at Colorado State University. Survey requests or questions, excluding parenthetical elaboration, were:

1. Please describe the nature and extent of your electrofishing experience.
2. What environments and under what environmental conditions have you sampled with electrofishing gear?
3. What species and size groups have you sampled or monitored with electrofishing gear?
4. What electrofishing equipment and techniques have you used?
5. Describe observations of adverse or injurious effects, especially with regard to endangered or related species.
6. Based on your experience, what recommendations would you offer for optimal electrofishing efficiency while minimizing injury to fish?
7. Please read the attached material abstracted from my report, which is still in preparation, and relate your response, thoughts, oversights, or criticisms on the content.

Eleven written responses were received–two from the lower basin, seven from the upper basin, and two from university graduate students without Colorado River Basin experience. Pertinent comments from discussions with two additional upper basin biologists were also considered in the following summary of responses.

Experience

The level of experience represented by survey respondents was extensive, both within and outside of the Colorado River Basin. Most respondents had at least 6 years of electrofishing experience and had served as crew leaders or supervisors; one had over 20 years of electrofishing experience. At least four took the U.S. Fish and Wildlife Service Fisheries Academy course on electrofishing. One taught a course on electrofishing. At least two had been involved in the development or modification of electrofishing gear.

Most respondents had electrofished in a variety of habitats, from large rivers to small streams and from major reservoirs to small lakes and ponds. Most electrofishing was done during spring through fall, but a few respondents also had experience electrofishing during winter in icy conditions. Temperatures during electrofishing were usually between 10° C and 20° C but were sometimes as low as 0° C or over 30° C. Most electrofishing, especially in the Colorado River Basin, took place in water conductivities of 300 to 1,500 µS/cm, but some respondents had experience with electrofishing in conductivities so low (down to 10 µS/cm) that salt blocks had to be used to increase conductivity or so high (2,000–5,000 µS/cm) that the power supply would shut down. Turbidity ranged from clear to very turbid, often moderately to highly turbid in the Colorado River Basin. Most respondents had experience with day and night electrofishing.

According to respondents, boat and raft electrofishing were typically used in Colorado River Basin studies and monitoring programs, but most respondents also had experience with wading systems (backpack, barge, or bank equipment). At least one had experience with fixed-position electrical grids and electric seines. Most systems were commercial (Coffelt, Smith-Root, and Georator). The Coffelt VVP-15 was mentioned most frequently. PDCs were the most frequently used currents, but a few respondents noted that when the situation allowed (e.g., low to moderate conductivities), they preferred to use DC. PDC parameters were seldom

reported, but two respondents stated that they used frequencies of 30, 40, or 60 Hz. One respondent never bothered with pulse width and frequency controls because the consensus seemed to be that these factors were not very important. When reported, voltages and currents for effective electrofishing, mostly in the Colorado River Basin, were reported as 200 to 350 V and 4 to 8 A, but some reported use of up to 12 A. One respondent noted that in very turbid waters, the system had to be "cranked up" as high as possible to bring the fish to the surface (a procedure since modified due to concern for injury). Use of AC was reported by only one respondent–many years ago in stream-wading situations. Electrode use was highly variable. Spheres were favored as anodes for boat and raft electrofishing, but dropper rings and single or multiple cables were also used. Metal boats, very long single or multiple cables, and spheres were typically used as cathodes. Some respondents changed electrode size or configuration according to the specific waters being sampled (e.g., smaller spheres for more conductive waters).

Observations of Harmful Effects on Fish

Some respondents noted that most electrofishing efforts were inadequately documented. Not only were notes on specific electrofishing gear, configuration, procedure, waveform, instrument settings, meter readings, and physical measurements frequently neglected, but also, records of electrofishing mortalities, injuries, and other harmful effects. Most respondents had to rely on their memories for recollections of such adverse effects. This matter has been rectified in some recent Colorado River Basin investigations (Valdez, personal communication). But even with comprehensive records, a few respondents suggested that because of differing environmental conditions, equipment configurations (especially type, number, and size of electrodes), and control box settings, it would be very difficult to correlate the incidence of injuries with those factors. Actual measurements of field intensities (voltage gradients) for determination of intensity distribution and field size would have taken into account many of these variables, but were overlooked in most Colorado River Basin investigations. Such data could be invaluable for comparing electrofishing results and adjusting power output and electrode size or configuration to maintain comparable fields within and between sites. In lieu of in-situ measurements, field-intensity distribution can be approximated by calculation if water conductivity, the size and shape of the electrodes, and peak output voltage, amperage, or power are known. Except for one investigation in which fish were dissected for contaminant assessments (Krueger, personal communication), no provision was made for assessment of spinal or other internal injuries caused by electrofishing. Most observations of injuries noted below and included in Appendix B were based solely on visible, external signs of injury (e.g., brands). Of course, until recently, few researchers suspected the occurrence of spinal injuries, and often even brands were not considered serious.

Respondents reported that in the Colorado River Basin they electrofished most species present in the areas sampled but that they rarely (in some cases never) experienced mortalities or injuries directly attributable to electrofishing, except for occasional brands. Several respondents have electrofished a wide range of size groups, from less than 4 cm to over 90 cm TL. Among fishes that were injured or branded, salmonids were found to be most susceptible (Appendix B). In one case, where fish were filleted for contaminant analysis, many captured rainbow trout and brown trout were found to have broken spinal columns posterior to the dorsal fin, whereas such damage was not observed for other species (Krueger, personal communication; Burdick, personal communication). Nearly all salmonids with damaged vertebrae also had externally obvious brands. Such brands were sometimes observed on over half of the trout collected. Brands or other injuries and deaths observed by respondents were frequently assumed to be caused by direct contact with anodes, especially cable anodes. No obvious signs of injury were reported for channel catfish, but two respondents noted that the species was extremely susceptible to tetany and slow to recover.

Electrofishing injuries or mortalities have been rarely reported for field-captured Colorado pikeminnow, humpback chub, or razorback sucker. Observations that have been recorded include brands (probably resulting from spinal injuries) in all three species, and at least one mortality and one occurrence of bleeding gills in Colorado pikeminnow (Appendix B). As further evidence that these endangered species do not appear to be seriously affected by electrofishing, some respondents noted that many electrofished and tagged specimens have been recaptured, sometimes repeatedly over a period of several years, and displayed no obvious aftereffects. Also, many electrofished and radiotagged specimens were successfully tracked for extended periods. Valdez (personal communication) suggested that with regard to long-term effects, physiological stress and damage to the nervous system may be the greatest impacts on these fish, but such effects would be difficult to assess.

One comparison of particular interest to many biologists who are concerned about spinal injuries, is whether Coffelt's new pulse-train current, CPS, has an advantage over typically used constant-frequency PDCs (usually generated via Coffelt's VVP-15 and Smith-Root's GPP

units) in reducing injuries while maintaining electrofishing efficiency. Contrary to many reports (Meyer and Miller, 1991, unpublished manuscript, 1991; Wyoming Game and Fish Department, 1991; Fredenberg, 1992, personal communication; Sharber et al., 1994), Trammell (personal communication) observed that there seemed to be proportionately more brands among rainbow trout and humpback chub collected with CPS in the Grand Canyon than with constant-frequency VVP-15-generated PDCs in the upper basin. However, Valdez (personal communication) noted that such comparisons are questionable without both units being used similarly in the same waters at about the same time.

With regard to experiences outside the Colorado River Basin, respondents submitted several notable observations. Gowan (personal communication) noted that among salmonids, electrofished specimens seldom showed external signs of spinal injury upon initial capture, but spinal injuries were sometimes evidenced a year later in fish that had stopped growing in the caudal region and became football-shaped. He also noted that the only significant electrofishing mortality he observed was among sculpins (Cottidae) captured in shallow riffles with outputs of 300 V or greater. The gills of these fish flared (probably in a state of tetany), and many fish died.

Pfeifer (personal communication) reported high mortalities among paddlefish electrofished with PDC in the Yellowstone and Missouri Rivers. Upon necropsy, the notochords of these fish were found to be completely ruptured. Obviously, spinal injuries are not restricted to fish with bony endoskeletons and vertebral centra. Pfeifer noted that the rivers electrofished were very turbid and suspected that many of the fish had made direct contact with cable anodes or were exposed to excessively high field intensities.

In Alaskan streams, Valdez (personal communication) reported a high incidence of brands among all sizes of Dolly Varden, pink salmon, and threespine stickleback electrofished with AC. However, many of these fish were recaptured a year or two later.

Two respondents used electrofishing to capture ripe fish for culture. Valdez (personal communication) reported taking a 9-kg female and several 0.9 to 2.2-kg male lake trout with no apparent ill effects on the subsequently released fish or their progeny. Egg survival was high. Pfeifer (personal communication) reported similar use of electrofishing to capture ripe walleye. He also observed no detrimental external effects on the brood fish or the percentage of eggs that hatched.

Many respondents suggested that handling of fish during and after netting probably has a greater effect on mortality and delayed recovery than the electric field. Overcrowding and stagnant, poorly oxygenated, holding water was recognized as a serious problem.

Respondents' Recommendations for Minimizing Harmful Effects

Approximately half the respondents suggested the following measures for minimizing harmful effects on fish:

1. Use the lowest power output that still provides for effective electrofishing (sufficiently large field for taxis and narcosis). In the Upper Colorado River Basin, Tyus (personal communication) suggested that amperage should normally be no more than about 5 or 6 A and if red shiner are being stunned, the amperage is too high. Gowan (personal communication) recommended that fish be observed following capture to ensure that they recover equilibrium within 1 to 2 min; if not, power should be reduced. Kinsolving (personal communication) suggested that the critical measure with respect to fish injury is voltage gradient, not output voltage or amperage per se. A simple home-built meter can be constructed (probe with appropriate voltmeter) and used to quantify or monitor field intensity in different waters and to locate hot spots in the field. Field intensity should be closely monitored in highly conductive backwaters and flooded tributaries. Hawkins (personal communication) noted that in spring, Colorado pikeminnow often occupy such habitats, wherein they are especially susceptible to electrofishing.

2. Use the least damaging current available, DC whenever circumstances allow; do not use AC. However, the occurrence of brands and extended tetany indicates that harmful effects are still a problem, even when using currents designed to be less harmful.

3. Use spherical electrodes and vary the number and size of spheres according to water conductivity and desired size and intensity of the field. However, Valdez (personal communication) noted that while spherical electrodes are theoretically superior to cables, he had not observed a significant difference in catch rate or the incidence of brands. Also, spherical electrodes limit the depth from which fish are drawn; Valdez (personal communication) suggested that spherical anodes and cable cathodes appear to be the best combination. Tyus (personal communication) recommended that anodes be kept high in the water to draw fish to the surface, where they can be easily netted.

4. Minimize exposure to the field and specimen handling–rapidly net fish before they get too close to the anode, and quickly, but gently, place them in oxygenated holding water. Tyus (personal communication) suggested that the foot-switch should not be closed continuously and that it should be released as soon as fish are observed near the anode. He also warned against overworking specific sites to maximize the numbers of fish captured. Buntjer (personal communication) cautioned that netters should not allow fish to remain in the net too long or

repeatedly dip fish back into an active electric field. Valdez (personal communication) noted that underwater lights improve netting efficiency.

5. Change the holding water frequently to ensure adequate dissolved oxygen and to avoid excessive temperatures on hot days; process the fish frequently to reduce crowding.

Some respondents emphasized the need to use trained personnel to properly operate the equipment under changing conditions and the best netters to quickly spot and remove fish from the electric field. Tyus (personal communication) emphasized that electrofishing trips should be scheduled to take advantage of conditions for the most efficient capture of target species (e.g., spring, when conductivity is relatively low and endangered species of fish are still in shallow, near-shore habitats). Electrofishing should not be attempted under turbid or windy conditions–the fish cannot be seen easily. Valdez (personal communication) emphasized the need to adequately document electrofishing operations and observations of harmful effects; those that have done so in the past have a valuable source of information. Analysis and summarization of such information might be useful in resolving the question of electrofishing injury, at least for the specific situations documented.

Conclusions

Electrofishing, the use of electric fields in water to capture or control fish, has been a valuable sampling technique in North America for over half a century, but it involves a very dynamic, complex, and poorly misunderstood mix of physics, physiology, and behavior. To be effective, the electric field generated around and between electrodes in water must be sufficiently strong at appropriate distances from the electrodes to elicit the desired responses by target fish. The size, shape, and nature of that field are defined by the distribution of electrical intensity which is determined largely by the peak electrical potential (voltage differential), type of current, and waveform generated between and around the electrodes; position, size, and shape of those electrodes; conductivity of the water; conductivity of bounding and surrounded media; and water-basin size and configuration.

What we know or believe about the responses of fish to electric fields is the cumulative result of many years of individual and often piece-meal research. In a much more concerted effort, many of these responses were intensively investigated and others revealed in the 1960's at the Barritz Hydrobiological Station in France (Blancheteau et al., 1961; Lamarque, 1963, 1967a, 1990; Vibert, 1963, 1967b; Blancheteau, 1967). However, many questions remained and the interpretation of some results was either difficult to understand or questionable. In a more recent attempt to better understand and explain the interaction between fish and electric fields, electrofishing has been treated as a power-related phenomena. According to this "power-transfer theory for electrofishing," the relationship between electrical power in water and in fish is a function of the ratio of conductivity of water to the effective conductivity of fish (Kolz and Reynolds, 1989a; Kolz et al., 1998). Even more recently, it has been suggested that the observed responses of fishes to an electric field, including twitches, taxis, narcosis, and tetany, are essentially aspects of the same phases of epilepsy (automatism, petit mal, and grand mal) that are observed in humans and other animals subjected to electroconvulsive therapy (Sharber et al., 1994, 1995; Sharber and Black, 1999). Most of the currently accepted or proposed concepts for explaining or better understanding the responses of fish to electric fields, and the mechanisms involved, need to be further explored, validated, refined, and integrated to advance the science and technology of electrofishing. This might be accomplished best through a well-coordinated, cooperative program for future electrofishing research.

Stress, injuries, and sometimes mortalities among captured fish are unavoidable consequences of electrofishing and most other collection techniques. Among the more effective gear and techniques available for collecting fish, biologists usually select those known to be least harmful, but comparative data on harmful effects are often lacking or inconclusive.

In many cases, especially prior to the late 1980's, electrofishing had been considered not only the most effective but also the least harmful means to capture fish, particularly moderate to large-size specimens. Despite occasional reports of substantial harm to fish, the relatively benign nature of electrofishing had been assumed because generally fish recovered quickly and few, if any, mortalities or external injuries were observed or reported. Also, the most frequently noted external effects, brands, were often dismissed by experienced electrofishers as harmless, temporary effects rather than as indicators of potentially serious spinal injuries or hemorrhages. But since the late 1980's, many investigators have shown that assessment of electrofishing injuries based only on externally obvious criteria can be highly inadequate.

Sharber and Carothers (1988) X-rayed and necropsied many large rainbow trout captured by electrofishing, found substantial numbers of spinal injuries and associated hemorrhages, and concluded that without such analysis, most of these injuries would go undetected unless they were especially severe. Especially severe spinal injuries or muscular hemorrhages can be represented externally by brands (particularly those that are in fact bruises),

bent backs, punctures, or abnormal swimming, but in most fish even severe injuries are not externally obvious. When electrofished specimens were similarly examined in subsequent investigations by other biologists (e.g., Holmes et al., 1990; Meyer and Miller, 1991; Fredenberg, 1992; Newman, 1992; McMichael, 1993; Hollender and Carline, 1994), they too documented in some species, especially salmonids, significantly, and sometimes dramatically, greater numbers of electrofishing injuries. As a result, new research was, and continues to be, funded to assess the extent of such injuries in specific applications, longer-term impacts, causes, and modifications to gear and techniques that might reduce harmful effects. Based on these studies, some agencies, institutions, and researchers have been reevaluating their use of electrofishing and instituting policies or guidelines to reduce the potential for injury. But we must better understand the problem, the factors involved, and how to minimize injuries.

Although verification through targeted research is still needed, the immediate cause of most spinal injuries and related hemorrhages appears to be strong myoclonic jerks (perhaps epileptic seizures referred to as automatisms) elicited by sudden changes in electrical potential, as when current beyond some threshold of intensity is switched on or off, pulsed, or alternated. As might be expected if this is true, comparative investigations generally have revealed that DC causes the fewest spinal injuries and hemorrhages and that low-frequency PDCs (<30 Hz, the lower the better) and at least one complex PDC (CPS) with a low inter-pulse-train frequency (15 Hz) cause substantially fewer spinal injuries and hemorrhages than higher-frequency PDCs and AC. Accordingly, these currents are recommended to minimize potential injuries. However, very low-frequency PDCs (e.g., 15 Hz) are generally considered less effective for inducing taxis and capturing fish than higher-frequency PDCs, perhaps because they, like DC, generally have higher field-intensity thresholds for the desired responses. More power might be needed to use them effectively.

The threshold magnitude of change in field intensity required to cause spinal injuries is probably the threshold for twitch, which in a heterogeneous field occurs in the zone of perception (reactive detection), well outside the zones of taxis, narcosis, and tetany, the effective portions of the electrofishing field. Accordingly, at least as many fish injured in the zone of perception are likely to escape the electric field as move into its effective zones for capture. Limited evidence suggests that field intensities greater than the threshold for sporadic muscular convulsions might not increase the frequency or severity of spinal injuries. If true, efforts to reduce the size of the most intense portions of the field, particularly the zone of tetany, might not have any impact on the incidence or severity of spinal injuries. But such efforts would still be beneficial in reducing potential for severe stress and mortality due to excessive fatigue and asphyxiation. Although as yet untested, increased duration of exposure under PDC would proportionally increase the number of pulses to which fish are exposed and thereby likely increase the probability of spinal injury. Regardless of exposure time and also as yet untested, sudden muscular convulsions, and therefore spinal injuries, are not likely to occur while fish are in a state of narcosis (petit mal) and probably not while in a state of full tetany (grand mal), although they may occur during transition to or between these states.

Except in very severe cases, electrofishing injuries in fish heal and seldom result in immediate or delayed mortality. Instead, most electrofishing mortalities appear to result from asphyxiation due to extended tetany or poor handling. However, electrofishing injuries may significantly reduce subsequent growth, at least until they fully heal. When sufficiently severe, spinal injuries may affect physical appearance or swimming ability. Still, even for highly injury-susceptible species, such as the salmoninae, significant effects at the population level are unlikely except in the case of very small or very extensively and intensively sampled populations, as is sometimes the case for threatened and endangered species.

Electrofishing can also affect reproduction and early life stages. In addition to or as a result of injuries, exposure of ripe fish to electrofishing fields can cause significant damage to, or premature expulsion of, gametes and sometimes reduces viability of subsequently fertilized eggs. Electrofishing over active spawning grounds can also significantly affect survival of embryos on or in the substrate if exposed during their more sensitive stages (prior to acquisition of eye pigment). Exposure of recently hatched larvae might not cause significant mortality but can reduce growth rates for at least a few weeks. Field intensity and duration of exposure appear to be the most critical electrical factors affecting embryos and larvae.

In the Colorado River Basin, electrofishing has been considered one of the most effective and least injurious techniques available for capturing the larger juveniles and adults of endangered and other large fishes. As elsewhere, relatively few fish other than salmonids have been reported to be killed or injured by electrofishing. But again, these fish had seldom been X-rayed or sacrificed for necropsy. Based on the few investigations in which endangered or native cyprinids were examined internally after exposure (adult Colorado pikeminnow and roundtail chub captured in two field studies and large juvenile Colorado pikeminnow, small juvenile bonytail, and small juvenile humpback chub exposed in laboratory experiments), neither spinal injuries nor other harmful

effects (mortality, severe hemorrhages, or for one species, subsequent short-term growth) appear to be a serious problem for these species using current electrofishing gear and techniques with DC or tested PDC waveforms and frequencies. However, experiments with endangered razorback sucker and their progeny suggest that at least ripe adults may be quite susceptible to electrofishing injuries and hemorrhages and that electrofishing them in this condition, especially over active spawning grounds, should be avoided. The survival and physical condition of endangered and other native cypriniforms (including razorback sucker) that had been electrofished in recapture and radiotag investigations also suggest that electrofishing injuries or mortality are probably not a serious problem. Even so, the sensitivity of the matter warrants a heightened awareness of the potential for electrofishing injuries, a continuing effort to minimize any harmful impacts by every practical means, and a readiness to adjust, alter, or abandon electrofishing techniques if and when potentially serious problems are encountered. Other sampling gear or techniques may need to be evaluated and adopted as appropriate.

Electrofishing is a valuable tool for fishery management and research, but when resultant injuries to fish are a problem and cannot be adequately reduced, we must abandon or severely limit its use and seek less harmful alternatives. This is our ethical responsibility to the fish, the populace we serve, and ourselves.

Responses to Specific Questions

The remaining conclusions of this investigation are best provided as responses to specific questions, mostly regarding endangered and other native species of the Colorado River Basin. Prior to the original version of this review, M. Yard (Grand Canyon Ecological Studies Aquatic Coordination Team, Bureau of Reclamation, Flagstaff, Arizona) assessed information needed by the National Park Service and assembled a list of questions to be addressed by this and, if need be, subsequent investigations. The questions (edited and reordered as appropriate) and answers follow:

1. Does electrofishing impact native species of fish as severely as rainbow trout?

With the probable exception of native salmonids and possibly ripe razorback sucker, evidence to date suggests that native species are not as susceptible to electrofishing injury as rainbow trout. But only one investigation (Meismer, 1999) directly compared the extent of immediate mortality and injury between rainbow trout and a native species. In that study, adult rainbow trout and similar-size subadult Colorado pikeminnow were exposed to several commonly used or recommended currents at field intensities corresponding to thresholds for typical responses. Except for one treatment with Colorado pikeminnow, the frequency of spinal injuries (all minor, Class 1, except in one Colorado pikeminnow) was insignificantly low for both species. However, rainbow trout experienced significant mortality (10 and 30%) when exposed to tetanizing intensities of 60-Hz, square-wave PDC and significant incidences of branding regardless of treatment, whereas Colorado pikeminnow experienced no immediate mortalities, no brands, and very few muscular hemorrhages regardless of treatment. Incidence of hemorrhages could not be assessed in the trout but, based on the frequency of brands, were probably common and at least moderate in severity.

Many Colorado pikeminnow, humpback chub, and razorback sucker have been captured by boat or raft electrofishing, some repeatedly in tagging studies. In over two decades of field research and monitoring studies, Colorado River Basin biologists reported very few incidents of immediate mortality, brands, or other externally obvious injuries in these fish due to electrofishing. Still, most of these fish were not X-rayed or necropsied for detection of spinal injuries, and except for a higher incidence of brands, the same can be said for trout.

2. Do we know the effects of electrofishing on all native fish species; if not, what fish would be most representative of humpback chub anatomically and physiologically?

No, but as discussed in this report and summarized in Table 2 and Appendix B, we now have some response or injury data for: adult roundtail chub, razorback sucker, cutthroat trout, mountain whitefish, and mottled sculpin; subadult Colorado pikeminnow (data on field-collected adults not yet reported); juvenile humpback chub and bonytail; and embryonic and larval razorback sucker. Electric fields can probably elicit somewhat similar responses in most, if not all, fishes, but all else being the same, the field-intensity thresholds and specific nature and degree of those responses will vary with species, size, and condition of the fish. Likewise for susceptibility to mortality and injury.

Roundtail chub, Gila chub, and bonytail are very close relatives of the humpback chub and are similar to it in morphology and physiology. Of these, roundtail chub is most common (only species of these not considered threatened or endangered) and has served as a surrogate for humpback chub in a field investigation of the injurious effects of electrofishing by Cowdell and Valdez (1994). For laboratory, raceway, or pond experiments, any of these species should be suitable surrogates if enough reared specimens of humpback chub are not available. However, Ruppert and Muth (1997) reported that response thresholds were notably lower for yearling humpback chub than

similar-size (but younger) bonytail. On the other hand, they also reported no spinal injuries for either species and no significant differences between them in the frequency of muscular hemorrhages.

3. What exists in the literature related to physiological responses and stress due to electrical stimulation?

Well over a hundred publications indexed by Snyder and Johnson (1991) include information on these matters. See the "Literature Cited" section at the end of this report and the bibliography by Miskimmin and Paul (1997a) for more-recent publications. All responses to electric fields, from reactive detection through tetany, are physiological. Even electrocution and the momentary but powerful convulsions believed to cause spinal and related injuries are physiological phenomena.

Exposure to tetanizing field intensity results in respiratory failure and synaptic fatigue, but if not exposed too long, fish usually recover normal breathing activity and equilibrium within minutes after removal of or from the field. However, excessive exposure to tetanizing currents can result in very long recovery periods or death. Fish may also cease respiratory movements under strong narcotizing field intensities, but remain relaxed and can survive longer exposures than under tetanizing currents.

Stress disrupts normal behavior and osmoregulatory functions. All capture methods and handling are stressful. Stress caused by electrofishing is similar to stress caused by hypoxia and intensive muscular activity. Reported changes in blood chemistry include increases in adrenal hormones, lactic acid, and blood clotting agents, which indicate overworked muscles and possibly traumatized tissues. Physiological recovery usually requires 6 to 24 h. However, some stresses, such as those related to physical injury, can persist for weeks or even months.

4. What are the physiological and anatomical effects of electrofishing on musculature, bone structure, blood, and reproductive organs?

According to Sharber and Black (1999), exposure of fish to an electric field of sufficient intensity overstimulates the central nervous system and results in epileptic responses. The level of central nervous system overstimulation, subsequent stimulation of muscles through the motor nerves, or failure of such causes the various behavioral responses observed when electrofishing (e.g., taxis, narcosis, tetany). Under certain conditions, particularly when potential of the field across the fish changes suddenly with sufficient magnitude (as when the current is switched on or off, pulsed, or alternated), some body muscles are stimulated to contract in very powerful convulsions. These presumably petit mal responses and possibly grand-mal responses of tetany (a sustained series of very rapid convulsions sometimes referred to as quivering or pseudo-swimming followed at a higher field intensity by a continuous convulsion making the body very rigid) can result in trauma to vertebrae, associated bones, muscle, and blood vessels. Vertebrae and associated bones can be separated, compressed, fractured, splintered, or misaligned (Figs. 1, 16, 18, and 19). Muscles can be bruised and torn, and blood vessels can be ruptured or blocked (Figs. 1 and 17). In extreme cases, such seizures may damage nerves and visceral organs. These internal injuries are often not obvious without X-rays or necropsy. When present, external signs include abnormal swimming behavior, bent backs (Figs. 3 and 4), brands (Fig. 2), and bleeding at the vent, gills, or base of the fins. Effects on physiological stress, including blood chemistry, are discussed in response to the preceding question.

Except when muscular convulsions are sufficiently severe to damage gonads or injure and force premature expulsion of nearly mature (ripe) gametes, general consensus is that there is probably no significant effect of electrofishing on the development or function of gonads or developing ova and sperm. However, specific data on such effects are limited and based mostly on salmonid broodstocks. Because fish are often targeted for sampling during the spawning season, the matter deserves specific investigation in wild fish, especially endangered species. Although there is some evidence to the contrary, electrofishing just prior to spawning might alter or inhibit subsequent reproductive behavior or physiology.

5. Are there differences in impact related to the age of the fish?

Yes. Early embryos have undeveloped neural and muscular systems, early larvae of many fish have incomplete skeletons and sensory systems, and all early life stages are substantially smaller than later juveniles and adults. As a result, not only are specific electrogenic structures (nerves and muscles) affected by electric fields either lacking or different than in older fish, but also the organisms as a whole are subject to much smaller potentials or voltage drops across the body. Taxis and narcosis are obviously not possible in the earliest embryos, and vertebral damage is not possible in recently hatched larvae of many species. Other effects, such as disruption of embryonic development, premature hatching, and even mortality at particularly sensitive stages, can occur.

Because age is reflected by size in juveniles and young adults, there may be size-related, and therefore age-related, differences in their susceptibility to electrofishing injuries. Some biologists reported that injuries to juvenile and adult fish are more frequent among larger specimens, whereas others found no consistent differences between age or length groups.

If poor condition is characteristic of very old fish of a particular species, these fish may differ from younger cohorts of the same species in their sensitivity to electric

fields and susceptibility to injury. This matter has not been addressed in the literature.

6. Are there any differences related to water quality?

Yes. Water chemistry determines its conductivity and affects physiology of fish, both of which influence the field-intensity thresholds for various responses by the fish. Also, very turbid waters make fish difficult to see and net, thereby reducing electrofishing efficiency and increasing the amount of time fish are exposed to the field before being captured. This, in turn, increases the probability of deaths and, in PDC and AC, injuries.

7. Is there an impact from exposure time and electrical frequencies?

Yes. Exposure time is especially critical in the zone of tetany, at least with regard to stress, fatigue, and mortality. In full tetany, active breathing ceases and death or damaging oxygen debt can quickly ensue because of sustained muscular tension. Breathing motions also cease in full narcosis, but skeletal muscles are relaxed and oxygen deficit accrues more slowly. Fish must be removed from zones of high field intensity as soon as possible and allowed to recover in well-oxygenated water. Based on very limited data, at least the lethal effects of PDCs appear to be exacerbated by increases in pulse frequency.

With regard to spinal injuries, exposure time does not appear to be a significant factor, at least for DC and AC. This is logical for DC if, as has been suggested, spinal injuries occur primarily with sudden changes in field intensity as when the field is switched on and off or pulsed. However, in PDC, the frequency of injuries generally increases with pulse frequency and might be expected to also increase with exposure time since both conditions increase the number of pulses to which the fish are exposed. The same might be expected for AC but limited evidence with respect to exposure suggests not. Pulse frequency also affects the strength of taxis and the field-intensity thresholds for various responses. Optimal frequencies for these responses vary with species.

8. What influences the incidence and extent of injury to fish besides the shape of the electrical pulse, power density (field intensity), and frequency of pulses; is one parameter more influential than another?

Susceptibility to electrofishing injury varies with species and, based on current data, is greatest for the Salmoninae (trout, char, and salmon). Other biological factors such as size and condition may also influence susceptibility.

Among physical factors, fish position and orientation in a heterogeneous electric field determine the field intensity to which the fish is subjected and, along with fish size, the voltage drop across the fish's body, and thereby its response to the field. Accordingly, position and orientation also determine whether a sudden change in field intensity is powerful enough to elicit a seizure and possibly whether the nature of the seizure is likely to cause spinal injuries. Although subject to minimum voltage across the body, fish perpendicular to the lines of current turn convulsively towards the anode and, based on limited data, are more likely to incur spinal injuries than fish parallel to the current.

Among electrical parameters other than field intensity, waveform, and frequency, the type of current has a strong influence on electrofishing injuries. DC generally causes less harm than AC or PDC. The possibility of detrimental voltage spikes when electric fields are switched on and off has been ignored, in part because some researchers believe the duration of such spikes is too short to have an effect, but this matter deserves specific investigation.

Field intensity is probably the most important electrical parameter affecting mortality, but above a certain relatively low threshold, it does not appear to be important with respect to spinal injuries. The only exception is that when it is high enough to induce a state of full narcosis or tetany, fish are probably not susceptible to the sudden convulsions resulting in spinal injuries. In PDC, pulse frequency seems to have the greatest effect on spinal injuries. Absence of pulses, as in DC, usually results in the least number of injuries, but they still can occur (up to 30% in some rare cases), probably when the current is switched on or off or the fish are removed (netted) from the field. The role of waveform or pulse shape remains unclear with contradictory results from various investigations.

9. What is the threshold level of injury for each fish species and can it be identified?

Defining injury broadly to cover most harmful effects of an electrofishing field, injury is caused primarily by two distinct conditions–tetany (grand mal) and the convulsive seizures of petit mal. Excessive exposure to currents at or above the threshold for tetany can result in severe stress, fatigue, and cessation of respiratory activity, possibly leading to death. Exposure to any current intensity at or above the threshold for twitch can elicit sudden and very powerful convulsions of the body musculature. These seizures can result in injuries such as compressed, broken, or misaligned spines; fractured or broken vertebrae, bones, or joints; ruptured blood vessels; and possibly a host of other traumatized tissues and organs. Such physical injuries have long been attributed to only the sustained contractions of tetany, but now it is uncertain whether they even occur during tetany, and if so, whether they differ in nature, frequency, or severity from those generated in less intense portions of the field. Outside the zone of tetany, some stress also occurs in the zone of reactive detection, stress and fatigue in the zone of taxis (especially in AC and PDC), and apnea in deep

narcosis, but aside from the stress and fatigue of physical injuries, these effects are generally mild and recovery is rapid. The threshold for spinal and related physical injuries can be identified as that for twitch and the threshold for severe stress, fatigue, and apnea as that for tetany. However, these thresholds vary with species, size of fish, water conductivity, type of current, and other factors.

10. Is power density the main parameter associated with electrotaxis, narcosis, and injury, or are these physiological responses independent of each other?

Field intensity, whether defined in terms of voltage gradient, current density (voltage gradient x water conductivity), or power density (voltage gradient x current density) is the primary electrical factor eliciting taxis, narcosis, and tetany in fish. Field-intensity thresholds for these responses tend to be lower in PDC and AC than DC, and in PDC appear to be inversely related to pulse frequency. Unlike taxis in DC, once the field-intensity threshold is achieved for taxis towards the anode in PDC, or oscillotaxis around the anode in AC, body flexures (swimming motions) appear to be, at least in part, a function of pulse or cyclic frequency. Once in a state of tetany, duration of exposure becomes the critical factor resulting in injurious fatigue or death due to asphyxiation; long exposure in a state of deep narcosis can also result in asphyxiation.

As noted above, sudden changes in voltage differential (field intensity) that occur when switching current or pulses on and off, if of sufficient magnitude relative to orientation of the fish, appear to be the cause of myoclonic jerks resulting in spinal and related injuries. At or above the relatively low field-intensity threshold for twitch, these sudden, potentially injurious, convulsions appear to be random and independent of other responses except when fish are actually in a state of narcosis or tetany. The incidence of these seizures and sometimes resulting injuries, may or may not increase with the magnitude of change in field intensity, but in PDC, and probably AC, they do increase with pulse or cyclic frequency and probably exposure time.

11. Does injury result from power densities that exceed those required for electrotaxis or that cause tetany?

Yes. Severe stress, fatigue, and hypoxia are caused by excessive exposure to tetanizing (or deeply narcotizing) currents and can result in death or possibly long-term physiological injury. Also, fish may be electrocuted and perhaps burned by extremely high field intensities or contact with an electrode. However, high field intensities are not prerequisite for spinal and related injuries caused by convulsive seizures. These physical injuries, and associated stresses, can occur anywhere in the effective field at or above the threshold for twitch in the zone of reactive detection.

12. What is the relation between narcosis and compression fractures?

There does not appear to be a specific relation between the two effects. Since fish in narcosis are fully relaxed it is logical to assume that they are no longer subject to the sudden convulsions believed to cause spinal or related injuries, including compression fractures. This also applies to fish in a state of full tetany unless the sustained muscular contractions characteristic of this state are sufficiently strong to compress and fracture vertebrae or burst blood vessels. The latter, historically assumed possibility has yet to be experimentally tested. It is likely that fish are still susceptible to convulsive seizures during transition to and from either narcosis or tetany.

13. Is there a relation between injury and type of equipment used?

Yes. Adverse effects and mortality resulting from tetanizing currents can be reduced by minimizing the effective zone of tetany. This can be accomplished by enlarging the electrodes, reducing power to the electrodes, or using DC with its higher threshold for tetany. Injuries resulting from momentary convulsions can be minimized by using DC rather than PDC or AC, reducing pulse frequencies in PDC to no more than 30 Hz (preferably less), or using Coffelt's CPS (or similar pulse trains if proven no more harmful).

If the rapidity with which pulses reach their peak voltage is a factor, use of waveforms with gradual rather than sharp rising pulses might reduce the incidence of injury. However, data from waveform comparisons are inconsistent and half-sine waveforms appear to be just as injurious as square, quarter-sine, and exponential waveforms. Voltage spikes often occur when current rises or falls very sharply (e.g., when DC is switched on and off and with each pulse in square-waveform and exponential PDCs). If such voltage spikes are ever shown to be a factor, they might be eliminated or minimized with electronic filters. But voltage spikes are not reported to be characteristic of half-sine waveforms, and these waveforms appear no less injurious than others.

14. Is there an impact on eggs and developing alevins?

Yes. Some investigators, particularly European authorities, have concluded that exposure to electric fields has no significant effect on developing eggs or larvae, but most, especially recent, investigations suggest otherwise. Most specific studies reviewed herein, including a recent study of razorback sucker, documented increased mortality among embryos exposed to electric fields and that this additional mortality increases with exposure time and field intensity. The effects appear similar to the effects of mechanical shock with embryos being

most susceptible to mortality prior to eyed-egg stages. Exposure late in the embryonic period might induce premature hatching. Nonfatal developmental effects, aside from premature hatching, have not been adequately investigated. There is little information on the harmful effects of electric fields on fish larvae and early juveniles, but published observations indicate that some species are more sensitive than others (e.g., mortality more likely for zander larvae than for trout larvae). Recently hatched razorback sucker larvae exposed to the same electric fields found to increase mortality among embryos suffered no significant effect on survival or behavior but did experience reduced growth rates during the subsequent 4 weeks. Obviously, it would be prudent to avoid electrofishing over active spawning grounds, especially for endangered species. Because larvae and early juveniles may be more susceptible to predation while recovering from exposure to electric fields, it might be wise to also limit use of electrofishing in discrete nursery habitats (e.g., backwaters and floodplains) heavily used by endangered species.

Some investigators reported significantly reduced production from ripe broodstock captured by electrofishing, but others reported no effect. The only investigation of such for an endangered species of the Colorado River Basin, razorback sucker, resulted in significantly reduced survival for embryos from parents exposed to electrofishing fields.

15. Can experiments be designed to quantifiably determine whether changes in an electrical system will reduce or eliminate spinal injury?

Yes. Several such experiments have been reviewed in this report, but much more can and should be done to confirm or establish specific cause-and-effect relations. The results of such investigations could lead to development of electrofishing gear and techniques that would further minimize adverse effects.

16. Are there means in use, or documented in literature that would reduce or eliminate injury to fish?

Yes, reduce but not eliminate. Where practical and when the power source is sufficient, use of well-filtered or straight DC is the best way to minimize spinal injuries and perhaps tetany-related effects. Researchers switching from PDC to DC may have to substantially increase field intensity and otherwise modify their electrofishing operation to maintain effectiveness. For example, some biologists working from boats use mobile or throwable anodes (Fredenberg, 1992) to take advantage of DC taxis. However, special safety concerns arise with the use of such techniques.

If DC is not practical and somewhat higher incidences of injury are acceptable, spinal injuries can be reduced in PDC by using the lowest effective pulse frequencies (preferably no more than 30 Hz) or Coffelt's CPS (other complex PDCs might be just as effective but have not been adequately tested). Unfortunately, very low pulse frequencies (e.g., 15 Hz) may produce insufficient taxis for effective electrofishing. Evidence regarding the relative harmfulness of different PDC waveforms (e.g., square vs. quarter-sine or exponential) is too limited and inconsistent for recommendations at this time.

There is some evidence that AC, especially 3-phase AC, might not be as bad as its reputation and that it is perhaps no worse than higher-frequency PDCs with regard to spinal injuries. However, until proven otherwise, AC should be avoided, especially in work with endangered fishes. Because comparative information on the effects of AC and PDC on spinal injuries is very limited, AC should be included in future research to evaluate harmful effects. When taxis to the electrode is not critical and if its harmful effects can be minimized (or accepted as when collected specimens are to be immediately killed or preserved), AC might still be a useful current.

With any type of current, tetany-related stress, fatigue, injuries, and mortalities can be minimized by reducing the zone of tetany immediately around the electrodes, and all harmful effects can be minimized by limiting the range of the zone of perception and removing fish from the effective portion of field as soon as possible. This can be accomplished by: (1) prudent selection of electrode size, shape, and configuration for the waters being sampled; (2) using the minimum power to those electrodes needed for effective electrofishing; (3) optimizing technique for capture and subsequent handling; and (4) only electrofishing when and where it can be done safely and effectively.

Within limits imposed by water conductivity and generator capacity, use of electrodes (or electrode arrays) with the largest practical surface area for each situation will minimize electrode resistance and the high-intensity zones of tetany around them. Generally, small-diameter cables should be avoided. Local hot spots of very high field intensity around the electrodes can be eliminated or minimized by selecting electrodes without sharp corners or edges.

With any electrode configuration, reductions in power output will reduce the zone of tetany, but it will also reduce overall field intensity and thereby the size of other response zones and possibly the effective range of the field. Electrode configuration and power output should be balanced such that the zone of tetany is minimized, the zone of narcosis does not extend beyond the reach of netters, and the zone of taxis is sufficiently large for effective electrofishing. The larger the electric field potentially perceived by fish, the greater will be the number

of fish likely to encounter it and be injured by it. Power output beyond that needed for effective electrofishing must be avoided. Methods for determining minimum effective power are described by Kolz et al. (1998).

Sampling techniques should minimize potential for exposure to tetanizing intensities and contact with the electrodes and facilitate rapid removal of fish from the electric field. Restricting use of electrofishing to near optimal conditions (e.g., relatively clear and calm or smooth flowing waters) will enhance the ability of netters to quickly spot and remove fish from the water. Holding facilities should be optimized to speed recovery and minimize further stress (e.g., frequently replaced water, oxygenation, avoidance of excessive crowding). Processing techniques should minimize handling and return recovered fish to the water as soon as possible.

17. What types of research identify the lower limits (thresholds) of field strength and pulse frequency for efficient electrofishing (good catch per unit effort)?

Controlled pond or field experiments. However, laboratory studies using homogeneous fields can simplify experimental design for these experiments by first identifying field-intensity thresholds for target species and size groups over a range of temperatures and conductivities for the currents to be tested (including PDCs covering a range of pulse frequencies). With this data and knowledge of conductivity and temperature conditions in the waters to be sampled, a range of potentially good electrofishing fields can be calculated and tested. Of course, the calculated electrofishing fields should be verified by actually mapping or spot checking field intensities before proceeding with experiments.

18. Are there threshold levels related to injury, and do these vary with species, sex, size, length, mass, and so forth?

Yes and probably. If muscular convulsions are the cause (or principal cause) of spinal and related injuries and the twitches observed well below field-intensity thresholds for taxis are such seizures, then the relatively low thresholds for twitches are also the thresholds for electrofishing (or electrical-field) injuries. Indeed, spinal injuries have been reported for Colorado pikeminnow and rainbow trout exposed to various currents at field-intensity thresholds for twitch. Similarly, field-intensity thresholds for tetany are the thresholds for the adverse effects of tetany, including death if sustained long enough. Thresholds for tetany under specific environmental and electrical conditions have been determined for many species, and lethal exposure times at tetanizing intensities have been approximated for a few species within certain size ranges. These response thresholds appear to vary at least somewhat with species, size (length or mass), and condition of the fish.

19. How comparable are previous studies when most researchers do not have the ability to use an oscilloscope to accurately determine field strength?

Not very. Without an adequate set of in-water electric-field measurements (either with an oscilloscope or peak-voltage meter), comparisons between studies, trips, or even sites within a trip can only be made on faith that the electrofishing controls and meters remained accurately calibrated and equipment was operating properly. Even when equipment is known to function properly, few researchers, especially in field investigations, record sufficient information to approximate field size and intensity. Without a reasonable approximation of field intensity and size, and knowledge of the specific waveform, frequency, and duty cycle utilized, results can neither be related to field and system (circuit) parameters nor properly compared with results from other studies or even different habitats within the same study. Failure to report whether output or field intensities are peak or mean (rms in AC) values and to recognize the difference between the two has confounded the results of many investigations. Electric fields with similar mean intensities can have substantially different peak intensities, and it is the peak field intensity that is believed to be biologically significant.

20. What studies have been conducted to assess delayed mortality resulting from electrofishing injury; how long have most fish been observed after exposure to an electric field?

Several studies held electrofished specimens for specified periods to assess delayed mortality (see above section on "Long-term Survival and Growth"). Monitoring periods for most of these studies ranged from a day to several weeks, but some have spanned several months to a year. Except when fish were seriously injured or fatigued, most of these studies reported little long-term delayed mortality attributable to electrical-field injuries. Some fish and game agencies routinely obtain broodstock by electrofishing and sometimes use electric fields in other hatchery operations (e.g., to anesthetize fish). Delayed mortality has not been reported to be a significant problem in these situations.

21. What species of fish have been used in electrofishing experiments; have any cyprinids been used other than grass carp and goldfish?

Many species, including marine fishes and many cyprinids, have been used in electrofishing experiments or field studies to assess responses and adverse impacts (see Appendix B and index to bibliography by Snyder and Johnson, 1991). However, in most cases, the objectives, methodologies, and conditions of these investigations differed such that the results of these studies are seldom directly comparable. Trout, particularly rainbow and brown trout, have been used most frequently.

Recent experiments have targeted response thresholds of and adverse effects on endangered species of the Colorado River Basin, specifically certain life stages of reared Colorado pikeminnow (Meismer, 1999), bonytail and humpback chub (Ruppert, 1996; Ruppert and Muth, 1997), and razorback sucker (Ruppert and Muth, 1995; Ruppert, 1996; Muth and Ruppert, 1996, 1997). Also wild specimens of another endemic native, the roundtail chub, were studied to assess spinal and related injuries (Cowdell and Valdez, 1994); likewise for wild Colorado pikeminnow that were field X-rayed and returned to the water in another investigation (Hawkins, personal communication). Other species represented in the Colorado River Basin that have been used in experiments or observations on the effects of electrofishing include: cutthroat trout, mountain whitefish, northern pike, common carp, goldfish, white sucker, channel catfish, flathead catfish, bluegill, green sunfish, largemouth bass, yellow perch, walleye, and mottled sculpin.

22. Does injury occur at the onset of electronarcosis or tetany, relative to body position in the field, or as the fish enters the electric field?

Spinal and related injuries resulting from convulsive seizures can occur anywhere in the field at or above the relatively low field-intensity threshold for twitch in the zone of reactive detection. If fish do not actually detect and respond in other ways to the field at still lower field intensities, then electrofishing injuries may occur even as fish enter the outermost reaches of the perceivable field. The convulsive seizures sometimes resulting in injuries are believed to occur primarily when fish are subjected to sudden changes in potential at or above that threshold, as when current or individual pulses are switched on or off or fish are quickly removed from or placed in the field. Whether these myoclonic jerks and potentially resulting injuries also randomly occur under conditions of constant current (DC) is not known, but if so, their frequency is normally much less than in PDC. Fish are probably susceptible to these sudden muscular convulsions and injuries during transition to and from narcosis and full tetany but probably not while they are in those states. Once fish are in a state of tetany, they are subject to severe stress, fatigue, and hypoxia depending on the magnitude of field intensity above the threshold for tetany and exposure time. Whether the sustained muscular tension of tetany can be strong enough to also cause spinal compressions, fractured vertebrae, or burst blood vessels has not been documented. The magnitude of voltage differential actually experienced by fish (across their bodies) would certainly vary with their position and orientation in the field. There is some evidence that upon a sudden change in voltage differential, fish oriented perpendicular to the lines of current suddenly turn much more sharply toward the anode and are more likely to suffer spinal injuries than fish oriented more parallel to the lines of current.

23. Is injury a relation of size, mass, length, and cross-sectional width, or is it species specific?

Based on field experiments in Alaska and Montana and controlled experiments elsewhere, there appear to be substantial differences in susceptibility of various species to spinal injuries caused by electrofishing. Size (at least length and width) affects the voltage differential a fish actually experiences (i.e., head-to-tail or across-body voltage) at any particular point and orientation in an electrical field, and therefore, the thresholds for various responses. Beyond the threshold level for electrically induced injuries (presumably that for twitch), the effect of size is uncertain. However, recent field studies on electrofishing injury indicate no significant size-related difference in injury frequency or severity among electrofished rainbow trout and brown trout between 20 and 58 cm TL (injuries were also observed among fish less than 20 cm TL, but data were insufficient for analysis of size-related differences). The relation between size and mortality is even less clear, but in at least one controlled experiment, size was not found to be a critical factor.

Future Research

Since the late 1980's, research on electrofishing and its injurious effects has expanded dramatically. Biologists have repeatedly confirmed the potential for electrofishing induced spinal injuries and hemorrhages and begun to explore the specific nature and causes thereof, as well as the relative susceptibility of different species. Fishery managers and biologists have begun to recognize such injuries as a potential problem and address it in their policy and practices. Manufacturers have developed new complex PDCs specifically to reduce the risk of such injuries. And new hypotheses have been advanced regarding "power transfer" to fish and the epileptic nature of their responses to electric fields. But much remains to be done.

Major technological advances to assure that the potentially harmful effects of electrofishing are minimized, while maintaining or improving its efficiency, will probably depend on a better understanding of the mechanisms involved, especially those resulting in injury. Before proceeding with intensive experimentation to this end, a thorough review of what is already known regarding the effects of electric currents on humans and other animals might be enlightening with respect to effects on fish and help focus future research. Sharber and Black (1999) suggested that the principal responses of fish to electricity are phases of epilepsy (Bozeman paradigm)

and essentially the same for all vertebrates. However, even the mechanisms involved in producing epileptic responses in humans and other animals are not fully understood. Also, discrepancies between the Bozeman paradigm and the previously accepted Biarritz paradigm must be explored and resolved. Perhaps it is time for a concerted, well-funded, national or international effort to better understand the responses of fishes to electric fields, document the specific mechanisms resulting in injury, and develop innovative gear, currents, and techniques to make effective electrofishing safer for man, fish, and other aquatic organisms.

In the meantime, work must continue on building a database of experimentally derived response thresholds and associated susceptibilities to injury for various species and size groups of fishes. Two major projects to this end are currently underway by Reynolds (personal communication; Standardized evaluation of electrofishing injury among North American freshwater sport fishes) and Miranda and others (Miranda, personal communication; Effects of electrofishing configuration on catch efficiency and injury rates of warmwater fishes). Such experiments should cover a variety of currents including DC, AC, and a range of typically used, currently recommended, and newly developed PDCs.

To supplement data from controlled experiments, standard practice in electrofishing, and especially research on electrofishing techniques and effects, should include observation and documentation of at least obvious injuries, abnormal behavior, and mortalities. When possible and consistent with research goals, biologists are encouraged to examine fish for internal injuries and monitor them for delayed mortality as well as for long-term behavioral and physiological effects. To better facilitate comparison and interpretation of results, biologists also are encouraged to more fully describe their electrode systems and document the physical and electrical parameters of their operations and experiments. Data should include water conductivity and temperature, output or, preferably, in-water measurements of field intensity, and if possible for PDCs, verification of waveform shape and pulse width and frequency. Output and field intensity values must be specified as either peak or mean values.

Recommendations

Interim Policy to Minimize Electrofishing Injury

The superintendent of Grand Canyon National Park, J.H. Davis, suggested in a 12 July 1990 memorandum to the GCES project manager that electrofishing for humpback chub be kept to a minimum and conducted in such a way as to minimize possible stress and injury. In the earlier version of this review (Snyder, 1992a), I suggested that this policy was warranted and should be extended on an interim basis to all endangered and native species of the Colorado River Basin until the harmful effects on those species are adequately documented and understood to justify changes. Since that review, the results of a few new experiments have provided limited evidence that endangered Colorado pikeminnow, native roundtail chub, and by inference, endangered humpback chub and bonytail are less susceptible to electrofishing injuries and associated hemorrhages than the Salmoninae (trout, salmon, and char). Although additional experiments and observations are needed to substantiate this conclusion, especially with respect to humpback chub and bonytail, evidence now appears to be sufficient (at least for the currents and PDC frequencies tested–DC, CPS, and 15- and 60-Hz PDC for Colorado pikeminnow and 40-Hz PDC for roundtail chub) to cautiously relax the minimal use policy and allow careful use of electrofishing for most monitoring and research efforts likely to contribute to recovery of these species.

In contrast to the situation for endangered cyprinids of the Colorado River Basin, policy minimizing use of electrofishing for the endangered razorback sucker remains warranted pending results of further experimentation. Results of the only experiment to date on adult razorback sucker suggest that at least reproductively ripe specimens may be quite susceptible to electrofishing injury, especially when using 60-Hz PDC.

Policy minimizing use of electrofishing is also warranted for rare, threatened, or endangered salmonids of the Colorado River Basin. The generally greater susceptibility of Salmoninae to electrofishing injury is well documented.

Based on this updated review, the following measures are recommended to minimize significant harmful effects of electrofishing:

1. Unless or until there is adequate evidence to the contrary, assume that available electrofishing techniques can cause enough injury to targeted or incidental species to be a potentially significant concern.

2. For species in which electrofishing injury is or might be a serious concern, especially if the fish are threatened, endangered, or otherwise of special concern, minimize use of electrofishing. When practical and effective, consider and use means for obtaining needed data without physical collection of fish (e.g., direct observation, cameras, scuba, sonic techniques) or by collecting fish with alternative gear and techniques likely to be less harmful.

2.1. Exceptions to this policy would include cases in which use of an alternative to electrofishing would jeopardize critical comparisons with past data, or when, during trial of or transition to an alternative, simultaneous use of both collection techniques is necessary to determine an acceptable correlation or data-conversion factor.

2.2. A review of literature comparing the effectiveness and harmfulness of electrofishing with other collection techniques would be useful. However, most published comparisons with alternative collection gear and techniques cover only sampling efficiency and seldom mention harmful effects. The bibliography by Snyder and Johnson (1991) lists about 80 such references. More-recent references are included in the updated bibliography by Miskimmin and Paul (1997a); a few are included in the "Literature Cited" section of this review.

2.3. Judgments regarding the injurious effects of some alternative gear and techniques may have to rely on the experiences of project biologists and outside contacts. Unlike many electrofishing injuries, injuries caused by most alternative gear for physical collection are more likely to be external and therefore more readily observed. However, this is an assumption and should be tested via X-ray and necropsy as it has been to assess internal injuries in electrofished specimens. Some alternative gear and techniques (e.g., entanglement nets) might be more stressful and cause greater mortality than electrofishing.

2.4. Used carelessly or improperly, any collection gear and technique can be harmful to fish, other aquatic organisms, or their habitat. Alternatives to electrofishing must also be used in such a way as to minimize significant harmful effects.

3. Regardless of target species, if electrofishing is the least harmful of practical and effective techniques for obtaining needed data or specimens, it should always be conducted in such a way and with such currents as to minimize potential for stress and injury as much as possible while maintaining sufficient effectiveness. In most cases, biologists will have to sacrifice use of currents and field intensities providing the greatest catch rates per unit time (e.g., high-field intensity using PDC at 60 Hz or greater). Even when susceptibility of the target species to electrofishing injuries is low, such may not be the case for other fishes that will also be subjected to the electric fields.

3.1. Exceptions to this policy include necessary investigations to assess susceptibility of a species to electrofishing injury or test gear, currents, or procedures to minimize adverse effects, and cases in which electrofishing can be used as a humane technique for reducing or eliminating populations of undesirable fish without significant harm to non-target species.

3.2. Based on latest information, update electrofishing equipment and procedures, including specimen handling, to ensure the least harm to captured fish.

3.2.1. Use the least harmful current available for effective capture of target fish.

3.2.1.1. Where practical, use DC.

3.2.1.1.1. Until strongly rippled DC is comparatively evaluated for harmful effects, DC produced from an AC source should be well filtered to make it relatively smooth.

3.2.1.1.2. Because of significantly higher field-intensity thresholds for desired responses, use of DC may require either a more powerful generator or acceptance of a smaller effective field.

3.2.1.1.2.1. Some of this limitation might be overcome by altering the electrofishing technique to take advantage of DC's good anodic taxis.

3.2.1.1.2.2. Experimental mobile or throwable anode techniques take advantage of anodic taxis and are reported to be effective (Nehring, 1991; Fredenberg, 1992), but they cannot be recommended unless specific safety procedures are followed (U.S. Fish and Wildlife Service policy is to not use a movable anode with a metal-hulled boat–Temple, personal communication).

3.2.1.2. If DC is not practical, use a low-frequency PDC (preferably 30 Hz or less, the lower the better), CPS, or other complex PDC proven as effective in minimizing spinal injuries. Kolz et al. (1998) provide a simple step-wise field procedure for determining the lowest combination of PDC frequency, pulse duration (width), and field intensity that will effectively catch fish. However, the impact of pulse duration on injury rates is uncertain with limited evidence that shorter pulse durations may be more harmful; the test procedure should be modified accordingly.

3.2.1.3. Whether warranted or not, AC is recognized by many authorities as the most harmful type of current used in electrofishing. Until proven otherwise, it should be avoided for most purposes.

3.2.2. Operate electrofishing systems at the lowest effective power setting with the largest practical electrodes to minimize or eliminate the zone of tetany around the electrodes.

3.2.2.1. Spherical, circular, or dropper array anodes are generally recommended rather than cables (especially single or paired, small-diameter cables).

3.2.2.2. Equipment for measuring conductivity and field intensity (voltage gradients) in the water should be available on each electrofishing trip to monitor equipment operation and adjust settings and electrodes for the desired size and intensity of the field. However, if the available electrode systems have been mapped for a specific output voltage and water conductivity, adjustments for differences in water

conductivity and the desired size and intensity of the anodic field can be calculated or graphed and a field-intensity meter may not be necessary except for recommended verification.

3.2.2.2.1. For in-water measures of field intensity, portable, field-durable oscilloscopes are preferred because they also can be used to monitor output waveforms and pulse duration, but commercial field-strength meters or similar home-built units based on voltmeters should be adequate if they accommodate the specific waveforms used.

3.2.2.2.2. Field-intensity measurements should be based on peak voltages. If the meters used can only measure average voltages, then pulse frequency, width, and shape can be used to calculate peak voltages.

3.2.2.3. Electrical output (voltage, amperage, or power) to the electrodes and electrode selection should be based on (standardized to) predefined field sizes and intensities that will maximize the range for taxis for the target species and size group, while minimizing the zone of tetany and limiting narcosis to a zone within easy reach of netters. Kolz and et al. (1998) provide procedures for standardizing applied power over a range of water conductivities.

3.2.3. Adjust the electrofishing technique in such a way as to net and remove fish from the electric field as soon as possible.

3.2.3.1. Select and position anodes such that fish are brought as near to the surface and as close to the netters as possible before narcosis. Maneuver the boat with the current in such a way as to improve netter access to the fish.

3.2.3.2. Position netters, and lighting at night, such that fish are more easily observed and captured; use polarizing glasses and other aids to minimize glare and reflections when electrofishing during daylight.

3.2.3.3. Avoid electrofishing when and where waters are rough, too fast for effective netting, or excessively turbid.

3.2.4. Optimize fish handling and holding facilities for fast recovery and least possible stress.

3.2.4.1. Fresh, well-oxygenated water must be provided, with a temperature not significantly warmer than that from which the fish were removed. Consider installation of a wire-mesh, Faraday-shield live tank through the bottom of electrofishing rafts or boats not used as cathodes (Sharber and Carothers, 1987). Isaak and Hubert (1997) described a live bucket to minimize holding injury and mortality when electrofishing small streams.

3.2.4.2. Avoid overcrowding captured specimens.

3.2.4.3. Some researchers suggest use of an anesthetic, such as MS-222, to keep fish calm while they recover or are processed (including X-rays). However, care must be taken to ensure that the anesthetic does not interfere with recovery. It might be wise to use anesthetic only in a second container for fish that have recovered equilibrium and normal behavior. Some anesthetics, including MS-222, can only be used in accord with U.S. Food and Drug Administration regulations.

3.2.4.4. Handle fish as gently and as little as possible. However, if a fish is very slow to recover breathing motions, it may be necessary to force fresh water over the gills with a hose or tube inserted in the mouth or gill cavity or by manually moving the fish back and forth in water.

3.3. Ensure that electrofishing equipment is well maintained and in prime operating condition and that personnel are adequately trained in its use and emergency procedures. Properly used equipment and attention to safety should minimize injury to fish and crew.

3.3.1. Governmental or other comprehensive and up-to-date guidelines for safe and proper use of electrofishing gear and techniques should be adopted and followed closely (e.g., guidelines by Goodchild, 1986, 1991; U.S. Fish and Wildlife Service, 1992; reviews by Hickley and Millwood, 1990; Goodchild, 1990; Lazauski and Malvestuto, 1990).

3.3.2. Because electrofishing systems are subject to extreme conditions, an oscilloscope (or other appropriate diagnostic equipment) should be used to check components for proper operation and calibration at least before, if not periodically during, each electrofishing trip.

3.3.3. Team leaders should be properly trained and certified in electrofishing theory and practice. An appropriate course and certification program is available through the U.S. Fish and Wildlife Service National Conservation Training Center (Branch of Aquatic Resources Training) in Shepherdstown, West Virginia (Kolz et al., 1998). The course is offered in a classroom setting at various times and locations throughout the country and as a correspondence course (internet web site—https://otis.fws.gov). Similar courses or related text material may be offered by other governmental agencies (e.g., Meyer and Miller, 1995), universities, or manufacturers.

3.3.4. Other electrofishing team members should be trained, if not certified, in the proper use of electrofishing gear and techniques for the specific sampling program (perhaps by the team leader with a refresher each season).

3.3.5. At least two, if not all, team members should be prepared to handle medical emergencies

through advanced planning for each trip (procedures and means to get help or reach medical facilities) and certified training in first aid and CPR (cardio-pulmonary resuscitation).

3.3.6. Periodic re-certification for electrofishing, first aid, and CPR should be required, perhaps every 5 years, to refresh and update knowledge with latest information.

3.4. Institute standardized procedures for documenting each electrofishing event and observations of adverse effects. This information is necessary to compare results between sites and studies, evaluate the conditions under which harmful effects continue to occur, and refine techniques to further reduce harmful effects.

3.4.1. Record output parameters (voltage and amperage, current type and waveform characteristics), description and placement of electrodes, water conductivity and temperature, and field intensity (voltage gradient at specified distances from the anode). It is especially important to note whether output and field intensity values are peak or mean (rms in AC) and whether water conductivity is ambient or standardized to 25° C.

3.4.2. Look for and detail all occurrences of injuries or abnormal behavior among individual specimens and associate with other recorded specimen-specific data or tag number; include at least species and length if not otherwise recorded. If distances of captures from the anode can be estimated, note that information as well. Dead fish should be frozen or otherwise preserved for subsequent examination.

Further Research on Electrofishing Injuries and Responses

The following are revisions of research recommendations originally outlined in Snyder (1992a) for continuation of Phase II of the Bureau of Reclamation's three-phase plan for addressing concern over the potential for electrofishing injuries among endangered and other native fishes in the Colorado River Basin. Phase II consists of controlled laboratory and field experiments to answer questions unresolved by past research. As listed in the Preface to this report, several investigations have been conducted since 1992 under Phase II, but much more remains to be learned and understood. If the potential for electrofishing injuries is significant (as it may be for razorback sucker and for the other endangered species when using PDC frequencies greater than already tested) and changes in current equipment and techniques are recommended to significantly reduce that potential, Phase III would test those recommendations in practical field operations. These research recommendations target fish and concerns of biologists and managers in the Colorado River Basin but can be modified to address similar concerns elsewhere.

Some of the suggested research parallels studies previously conducted for other species, particularly rainbow trout and brown trout. Accordingly, when possible for comparative purposes, rainbow trout should be treated as one of the test species.

The first question is whether the species of concern are likely to be significantly injured by currently used electrofishing gear and techniques under all environmental conditions likely to be sampled. If not, the matter of electrofishing injury to endangered fishes in the Colorado River Basin becomes a non-problem for those gear, techniques, and environments, and further research either becomes unnecessary for recovery concerns or can be redirected toward other basin fishes that may be significantly affected. Because endangered species recovery requires consideration of the entire ecosystem, adverse impacts of electrofishing on other native species are also a concern. Even if electrofishing injuries are likely to be significant, that incidence of injury might be acceptable if there are no better alternatives for obtaining information critical to recovery efforts. Unless already known to be less or no more harmful than currently used electrofishing gear and techniques, or sampling conditions, each prospective change in electrofishing gear, technique, or environment sampled should be tested for harmfulness before the change is adopted.

Recommendations for continuing Phase-II research are:

1. Field and pond studies. Continue determining whether and to what extent electrofishing gear and procedures used in the Colorado River Basin cause physical injury to endangered or other native fishes. The three suggested approaches to this end (1.1, 1.2, 1.3) are intended to provide complementary information, but if necessary they could be treated as alternatives.

1.1. Appended investigations. As part of specimen processing for endangered and other selected species in ongoing field investigations or monitoring programs utilizing electrofishing as a capture technique, include thorough external examination for signs of injury, X-ray analysis for vertebral and other skeletal damage when possible, and necropsy of any mortalities or statistically useful subsets of non-endangered species sacrificed for assessment of internal injuries. This has been done for Colorado pikeminnow, but the results have not yet been reported (Hawkins, personal communication). This approach assumes that the X-ray exposures will cause no significant harm to wild fish or their offspring (an assumption that still needs to be

experimentally verified). Regardless of use of this approach for assessment of electrofishing injuries, thorough external examination of all specimens and documentation of observed signs of injury should become standard procedure for all investigations using electrofishing (or other) gear and techniques.

1.1.1. For thorough external examination, document and describe in detail all external signs of physical injury including brands, bent backs, punctures, and bleeding at the vent, gills, fin bases, or elsewhere.

1.1.2. For X-ray analysis:

1.1.2.1. Supplement the usual field crews with a separate team of properly trained and equipped biologists to expedite field radiography of fish using a portable X-ray machine and ensure the safety of all personnel.

1.1.2.2. Label each X-rayed fish such that radiographs can be associated with recorded field and analysis data for that fish.

1.1.2.3. Document the presence and severity of spinal injuries using to Reynolds' (1996) criteria (Table 3). Be aware that minor vertebral fractures may be difficult to assess in X-rays of small fish.

1.1.3. For necropsy of electrofishing mortalities (including specimens that are not likely to survive), specimens sacrificed for other purposes (e.g., contaminants analysis), and statistically useful subsamples of selected non-endangered species sacrificed for this purpose:

1.1.3.1. Document the presence and severity of spinal damage and associated hemorrhages using Reynolds' (1996) criteria (Table 3).

1.1.3.2. Document other external and internal damage or anomalies following Goede and Barton's (1990) necropsy-based procedures and criteria for fish health and condition profiles (HCP; blood tests can be omitted).

1.1.3.3. Fish can be iced or frozen and processed at a later time and more convenient location.

1.1.4. If possible, record the behavior and condition of fish as they are netted–for example, active (automatism, taxis; note whether swimming motions are normal or abnormally rapid), unconscious and limp (petit mal, narcosis; note whether breathing motions have ceased), or unconscious and stiff (grand mal, tetany) or quivering (partial tetany, transition from narcosis to full tetany).

1.1.5. Observe and record any difficulties in recovery from narcosis or tetany (note nature and duration of problem and special measures taken to aid recovery), mortality if the fish fail to recover, and any abnormal behavior once breathing motions and equilibrium are reestablished.

1.1.6. Also record:

1.1.6.1. Date, time, water temperature, conductivity, turbidity, depth, habitat type and other environmental conditions at each site.

1.1.6.2. Electrofishing electrode configuration (type, size and placement), output voltage (note whether peak or mean values), type of current and waveform (shape), pulse or cyclic frequency (if PDC or AC), and pulse width or duty cycle (if PDC).

1.1.6.3. In-water measurements of field intensity at standardized locations relative to the electrodes and vessel (again note whether peak or mean values).

1.1.6.4. Sampling strategy, including average and maximum exposure time per "switch-on" event and for each effort as a whole.

1.1.6.5. When electrofishing parameters and techniques are standardized for specific environmental conditions (temperature, conductivity, depth, habitat type) they need be measured only once under each set of conditions during a trip, except for continual monitoring of output and periodic checks of field intensity.

1.1.6.6. Such thorough documentation should be standard practice for all electrofishing operations, regardless of purpose.

1.1.7. If species of trout or other Salmoninae (which are especially susceptible to spinal injuries) are captured in statistically useful numbers, they should also be examined and analyzed for comparative purposes.

1.1.8. If sufficient numbers of the same species and size classes are collected in existing programs by other gear for statistically useful comparisons, they should be similarly examined and documented.

1.2. Special field studies. Conduct special field studies, independent of ongoing investigations, to specifically document the incidence and severity of electrofishing injuries in selected fishes that can be sacrificed, especially native species chosen as surrogates for the endangered species (e.g., roundtail chub and flannelmouth sucker). One investigation of this type has been conducted by Cowdell and Valdez (1994) using adult roundtail chub as a surrogate for humpback chub. The investigations of Sharber and Carothers (1988, 1990) on adult rainbow trout, which initiated recent concern over electrofishing injuries, were also of this type.

1.2.1. Electrofishing gear and techniques should be comparable to those normally used and prospectively used in the basin.

1.2.2. Examine all target specimens as per item 1.1.1. above, then euthanize and ice or freeze for subsequent laboratory analyses by X-ray radiography and necropsy as per items 1.1.2.2., 1.1.2.3., 1.1.3.1., and 1.1.3.2. above. X-rays could be taken by or at a cooperating educational or medical facility. If possible, include statistically useful subsamples by size class.

1.2.3. Observe and document condition upon capture, difficulties in recovery, and abnormal behavior upon recovery as outlined above under items 1.1.4. and 1.1.5., and record environmental and electrical parameters as per item 1.1.6.

1.2.4. If species of trout or other Salmoninae (which are especially susceptible to spinal injuries) are captured in statistically useful numbers, they should also be examined and analyzed for comparative purposes.

1.3. Controlled pond experiments. Conduct controlled electrofishing experiments in large ponds to document incidence and severity of electrofishing injuries on hatchery-reared endangered fishes, preferably fish not previously subjected to electric fields.

1.3.1. Fish should be tagged for individual identification and examined for pre-existing injuries or anomalies based on pretrial X-rays and detailed external examination.

1.3.2. Follow procedures as suggested for approach 1.2. above.

1.3.3. Fish remaining in the ponds after electrofishing should be collected by other means (e.g., seining) as soon as possible and processed similarly for comparison. Assuming the ponds were intensively sampled by electrofishing, most of these specimens would likely represent fish that were subjected to electrofishing fields but escaped capture.

2. Laboratory experiments on juvenile and adult fish. Conduct laboratory experiments to document and compare the injurious effects and induced responses of currently used and potentially less harmful electrofishing waveforms on endangered fishes (or surrogates) and other species of concern in the Colorado River Basin. Identify waveforms, electric-field characteristics, and conditions (from among those tested) that will minimize injurious effects, but still elicit sufficient taxis and narcosis for effective electrofishing. Conduct experiments initially in homogeneous electric fields and follow up, if appropriate, with comparable experiments in heterogeneous fields. As of this review, limited versions of such experiments have been conducted only with small juvenile humpback chub and bonytail (Ruppert, 1996; Ruppert and Muth, 1997) and subadult Colorado pikeminnow, and for comparison, similar-size adult rainbow trout (Meismer, 1999).

2.1. Currents and waveforms to be tested.

2.1.1. Currents and waveforms typically used in the Colorado River Basin or believed to reduce the incidence of injury.

2.1.1.1. Quarter-sine, 120-Hz PDC with 7-ms pulses (80% duty cycle).

2.1.1.2. Square, 80-Hz PDC with 5-ms pulses (40% duty cycle).

2.1.1.3. Square and quarter-sine, 60-Hz PDC with 4-ms and 13-ms pulses (25% and 80% duty cycle, respectively).

2.1.1.4. Square, 30-Hz PDC with 4-ms pulses (12% duty cycle).

2.1.1.5. Coffelt's CPS, a pulse train of three 240-Hz, 2.6-ms pulses every 15th of a second (12% duty cycle).

2.1.1.6. DC (filtered and conditioned from rectified AC).

2.1.2. Single-phase, 60-Hz AC and three-phase, 180-Hz AC should ultimately be tested for comparative purposes.

2.1.3. Others of interest (possibly including other specially developed complex PDCs such as Smith-Root's sweeping waveforms).

2.1.4. Waveforms for the above need to be clean and well-defined. If voltage spikes are found to be a significant component of a typically used current or waveform, both it and the clean version of the waveform should be tested separately and compared.

2.2. Variables to be considered in experiments with each waveform. Except for field intensity, initial experiments should be conducted with these variables held at a fixed level that approximates typical conditions when electrofishing in the Colorado River. Subsequent experiments should be conducted over a range of values for each variable (at least two more levels), one variable at a time, to assess the effects of those variables on injuries and responses.

2.2.1. Field intensity (voltage gradient) and exposure time.

2.2.1.1. To simulate heterogeneous electric fields gradually moving over fish (or fish in taxis moving towards anodes), experiments should be run with voltage gradient continuously increased at a steady rate from a near zero value (e.g., Meismer, 1999). A variable-speed motorized control of voltage is recommended to ensure a constant rate of increase in field intensity. Individual tests should be concluded immediately after the response being tested is achieved either by switching off the current or gradually reducing field intensity back to zero. The latter eliminates the possibility of injury caused by the sudden change in voltage as the field is switched off (perhaps especially important when testing DC). Tested responses should include reactive detection (twitch), taxis, narcosis, and tetany; a level of field intensity well above the threshold for tetany is also recommended for comparison. At least in initial or preliminary experiments, different rates of voltage gradient increase should be tested, thereby increasing or decreasing exposure time to the progressively increasing field intensity.

2.2.1.2. To simulate stationary electric fields positioned over fish when the current is switched on, the above experiments should be repeated at fixed voltage-gradient levels over a range of exposure times (e.g., Ruppert and Muth, 1997 except their experiments were conducted with a single fixed exposure time). The current should be switched on and off at the preset intensity level after the fish are appropriately positioned in the water. The selected voltage-gradient levels should be slightly greater than or bracket response thresholds

suggested above. Use of levels less than the response thresholds when tightly bracketed, would document whether threshold levels are in part dependent on exposure time. One level well below the threshold for reactive detection and one well above full tetany should be included for comparative purposes.

2.2.2. Water conductivity between 10 and 2,000 µS/cm; 500 µS/cm would be a good choice for initial experiments because it is median to the range of conductivities typically experienced in Colorado River Basin endangered-fish investigations. Ultimately, tests to determine field-intensity response thresholds should be conducted in at least three or four widely ranging freshwater conductivities (at least 10, 100, 500, and 1000 or 2,000 µS/cm) to provide threshold data over a range of conductivities. In addition to documenting response thresholds relative to conductivity, the resulting data could be used to determine for these fish the power-transfer relations postulated by Kolz (1989a).

2.2.3. Water temperature between 5 and 25° C; 15 or 20° C would be a good choice for initial experiments.

2.2.4. Fish size groups between 2 and 50 cm. Because fish under 10 cm are usually easier to handle and obtain in quantity, they might be a good choice for initial experiments (Ruppert and Muth, 1997). However, they may be more difficult to necropsy, and their X-rays may not be as easy to analyze as those of larger fish.

2.2.5. Fish orientation. Experiments should be conducted initially with fish oriented (or maintained) in various directions (e.g., toward the anode, toward the cathode, transverse to both, and positions between these). Position or changes in position during an exposure could significantly affect experimental results. Sharber (personal communication) reported a much greater incidence of spinal injuries among trout held perpendicular to the lines of current than parallel to the current.

2.3. Fish species.

2.3.1. Initial experiments should be conducted on surrogates for the endangered species and rainbow trout, the latter for comparison and verification of previous observations on that species.

2.3.2. Once the critical ranges for experimental variables are narrowed as a result of the initial experiments, more focused experiments can be conducted on other species, including endangered species if expendable hatchery-reared specimens are available. If the effects, responses, and response thresholds for the endangered species are very similar to those for the surrogate species, only enough endangered-species experiments need to be conducted to support that conclusion, and remaining surrogate-species results can be extrapolated to the corresponding endangered species.

2.3.3. If differences in response thresholds and susceptibility to injury are found between hatchery-reared and wild stocks of the same species, these differences should be documented and considered in the interpretation of results. Such differences have been observed for trout (Sharber, personal communication; Fredenberg, personal communication).

2.4. Responses and injuries.

2.4.1. Each experimental specimen should be marked or tagged for individual identification, measured, examined for external anomalies, X-rayed (to document any existing spinal anomalies), and acclimated to the water temperature and conductivity in which it will be tested.

2.4.2. Responses for each tested fish should be recorded on video tape with specimen data, a time index, and the level of variables tested. Such documentation will allow repeated review of questionable observations and independent analyses.

2.4.3. After each trial, fish should be observed carefully for rate of recovery and abnormal behavior, examined for external signs of injury, then X-rayed for spinal injuries and dissected for related internal injuries according to procedures outlined above for mortalities and sacrificed fish in field experiments (item 1.2.2.).

2.5. Homogenous versus heterogenous fields. Experiments should be conducted initially in homogeneous fields (rectangular tank with full cross-sectional electrodes) to minimize confounding factors and allow comparison with published data. When waveforms or other experimental factors significantly affect either injuries or typical responses, experiments should be repeated in heterogeneous fields (e.g., quarter-circular tank with one full-depth electrode at the apex and the other full-depth electrode lining the outer wall, or perhaps better yet in an open-water setting such as a pond with standard electrofishing electrodes).

2.5.1. In heterogeneous fields, fish should be tested in anodic and cathodic fields. Effects in the cathodic field have been largely overlooked in past research, especially with regard to injury, and they may differ from effects in the anodic field.

2.5.2. These experiments will establish the relation between responses and thresholds observed in homogeneous and heterogeneous fields.

2.5.2.1. If the relation is well defined and consistent, future experiments with other species may only need to be conducted in homogeneous fields.

2.5.2.2. If the relation is inconsistent or difficult to define because of continuously varying voltage gradients, future experiments for field-applicable thresholds may be limited to heterogeneous fields.

2.6. Application of results. If these experiments demonstrate that some electrofishing currents, waveforms, and conditions are less harmful than others to endangered or surrogate species, while still eliciting

sufficient taxis and narcosis for effective electrofishing, then electrofishing gear and techniques used in recovery and fishery investigations should be modified accordingly. Based on response threshold data, it might also be possible to define optimal field sizes and intensities for consistent electrofishing over a wide range of water conductivities and temperatures while minimizing potential for harm. A simplified set of experiments could be designed for similarly determining optimal electrofishing fields for other species.

3. Laboratory experiments on spawning adults and early-life stages. Conduct a series of experiments on the effects of presently used and potentially less harmful electrofishing fields on the spawning and early life stages of endangered species (or surrogates), other native species of concern, and rainbow trout (for comparison with existing observations).

3.1. Effects on spawning adults. Determine the adverse effects of electrofishing fields on the reproductive capability and behavior of fish exposed while in or approaching a state of spawning readiness (e.g., in part for razorback sucker, Muth and Ruppert, 1996). Fish are sometimes targeted for electrofishing as they aggregate for or begin spawning.

3.2. Effects on eggs and larvae. Determine the effects of these electrofishing fields on developing eggs and larvae in and out of simulated substrate (e.g., for razorback sucker out of substrate, Ruppert and Muth, 1995; Ruppert, 1996; Muth and Ruppert, 1997). Adults are sometimes electrofished over spawning grounds.

3.3. Responses and thresholds for larvae and early juveniles. Document responses and response thresholds of protolarvae, mesolarvae, metalarvae, and early juveniles, and determine the sizes at which these fish begin to respond like older fish and incur spinal injuries. Larval and YOY fish are likely to be present in many habitats that are electrofished for larger juveniles and adults.

4. Long-term effects of injuries. If incidence of electrofishing-induced spinal (or related) injuries is significant for endangered species, and changes in technology (e.g., current and waveform) and technique are unacceptable or do not sufficiently reduce the incidence of injuries, then conduct a series of 1 year or longer pond investigations to assess subsequent effects of the injuries on survival, growth, condition, and, if possible, reproductive viability.

4.1. Ponds. Each pond should include approximately equal numbers of treatment and control fish.

4.2. Treatments. Treatment fish would be intentionally injured (vertebral fractures or misalignments) by electric fields and X-rayed for verification and subsequent comparison. Also consider a second set of treatment fish, those subjected to the electric field but not sustaining a detectable injury.

4.3. Monitoring. All fish should be periodically captured using nonelectrofishing techniques and monitored for injury healing, survival, growth, condition, and reproductive state.

4.4. Results. If most electrofishing-induced injuries do heal and subsequently have no detectable effect on survival, growth, condition, or reproductive behavior, then the matter of electrofishing injuries is not critical with respect to population management and recovery of the species.

4.5. Assessment of past damage. It might be desirable to conduct these experiments even if changes in standard electrofishing technique do reduce the harmful effects; the results might help assess the extent of damage done to endangered populations by past electrofishing activities.

5. Investigations into causes and mechanisms with integration of knowledge for other vertebrates. Employing or in consultation with electro-physiologists, compare and contrast known or hypothesized effects of electricity on fish with those on other vertebrates, then design and conduct laboratory experiments, beyond the preceding, to confirm or determine the specific causes and mechanisms involved in electrofishing responses and injuries.

6. Improvements to electrofishing gear and techniques. Based on results of the above suggested research, refine, develop, and test new electrofishing gear and techniques to help minimize harmful effects while maintaining the size and intensity of electric fields needed for consistently effective electrofishing. Possibilities might include:

6.1. Improved control box meters and displays. Provide accurate voltage meters and ammeters as standard components of all electrofishing systems for monitoring peak (as well as mean) electrical output. If the meters are digital, a special circuit could be incorporated to calculate and also display output power. For PDC, displays of accurately measured pulse frequencies and duty cycles or pulse widths should also be provided.

6.2. Special meter and probe for monitoring electric fields. Develop a special electrofishing field meter with omni-directional probe for mapping electric fields and monitoring peak voltage gradients, ambient water conductivity, and water temperature at standardized locations. (Kolz, 1993, suggested that a voltage-gradient probe could be designed for simultaneous measurement in both horizontal and vertical planes and used with a meter that would add these components and display the resultant magnitude of voltage gradient. However, such a probe would still have to be rotated to determine direction of current flow and maximum voltage gradient.)

6.2.1. The probe, perhaps a spherical apparatus suspended by gimbals and oriented magnetically like a compass, would automatically detect

the orientation and direction of maximum current (principal vector, lines of flux) and sense the peak voltage gradient along that vector. It would also provide sensors for conductivity and temperature.

6.2.2. The combination field meter should accurately measure and display peak voltage-gradient, direction of the current in both horizontal and vertical planes, ambient water conductivity, and water temperature. Circuitry could be included to calculate and display peak power density. Incorporation of a small digital oscilloscope for measuring and displaying peak voltage gradient would have the added benefit of providing specific waveform information (e.g., shape, including presence of spikes, frequency, pulse width). The meter should be able to accommodate or be modified for a variety of electrofishing currents and PDC and AC waveforms.

6.3. Automated control of field intensity for boat electrofishing systems.

6.3.1. Such a system might be useful when electrofishing highly variable habitats with different water conductivities (e.g., when moving from deeper open waters to very narrow, shallow coves with silt substrate, shallow riffles with cobble, or across or into the mouths of tributaries with significantly different conductivity or temperature). When sampling more uniform habitats, such a system might be superfluous.

6.3.2. Using a fixed or standard-position sensor for voltage gradient and water conductivity (e.g., the above mentioned omni-directional probe fixed 30 cm below the surface and 1 m from the center of the anode towards the boat), a digital peak voltage-gradient meter or oscilloscope built into the control box, and a control-box mechanism for automatically controlling output voltage to maintain a preset voltage gradient at the probe.

6.3.3. The preset voltage gradient at the position of the probe might be selected by calculation, table, graph, or built-in computer program to provide the optimal electrode-specific field-intensity map for the target species based on its response thresholds (e.g., a distribution of field intensity that would provide for initiation of taxis and narcosis at some optimal distance from the anode).

6.4. Improved electrodes. Design electrodes to minimize tetany-related injury and stress to fish and optimize the effective portion of the electrofishing field.

6.4.1. In addition to using the largest practical electrodes, shield fish from direct contact with, and the very highest field intensities immediately around, those electrodes by surrounding or covering the electrodes with a deep, but fine grid of non-conductive material (plastic).

6.4.2. Design boat-electrofishing anodes to semi-freely float by suspending them from or incorporating a floatation devise to maintain the effective portion of the anodes just under the surface of the water and provide some mechanism to maintain each anode in a fixed position in front of the boat. As electrofishing boats move through the water and personnel move about on the boats, they tend to bob up and down with conventional boom-suspended electrodes either moving deeper into the water or partially rising above the surface, thereby reducing the electrodes' effective surface area. Anodes suspended from booms also change position relative to the front of the boat as boats turn or surge forward or backward. Such changes in the relative position and submergence of anodes can dramatically affect the effective size of the electric field and distribution of field intensity therein.

6.4.3. Design hemispherical (or half-submerged spherical) anodes or alternative high-surface-area electrodes with no upward-facing surfaces, and no sharp corners or edges, to efficiently direct all of the electric field horizontally and downward. Spherical and certain other types of electrodes submerged near the surface direct a significant portion of the field upward to the surface where it is effectively wasted.

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Appendix A. Scientific names and families of fishes referenced by common name in this report. Names follow Robins et al. (1991a,b).

Common name	Scientific name	Family
American eel	*Anguilla rostrata*	Anguillidae
Arctic grayling	*Thymallus arcticus*	Salmonidae
Atlantic cod	*Gadus morhua*	Gadidae
Atlantic salmon	*Salmo salar*	Salmonidae
black crappie	*Pomoxis nigromaculatus*	Centrarchidae
black bass	*Micropterus* species	Centrarchidae
blue catfish	*Ictalurus furcatus*	Ictaluridae
bluehead sucker	*Catostomus discobolus*	Catostomidae
bluegill	*Lepomis macrochirus*	Centrarchidae
bonytail	*Gila elegans*	Cyprinidae
brook trout	*Salvelinus fontinalis*	Salmonidae
brown bullhead	*Ictalurus nebulosus*	Ictaluridae
brown trout	*Salmo trutta*	Salmonidae
bull trout	*Salvelinus confluentus*	Salmonidae
bullhead	*Cottus gobio*	Cottidae
burbot	*Lota lota*	Gadidae
channel catfish	*Ictalurus punctatus*	Ictaluridae
chinook salmon	*Oncorhynchus tshawytscha*	Salmonidae
chum salmon	*Oncorhynchus keta*	Salmonidae
coho salmon	*Oncorhynchus kisutch*	Salmonidae
Colorado pikeminnow	*Ptychocheilus lucius*	Cyprinidae
common carp	*Cyprinus carpio*	Cyprinidae
common shiner	*Luxilus cornutus*	Cyprinidae
creek chub	*Semotilus atromaculatus*	Cyprinidae
crucian carp	*Carassius carassius*	Cyprinidae
cutthroat trout	*Oncorhynchus clarki*	Salmonidae
Dolly Varden	*Salvelinus malma*	Salmonidae
dragonet	*Callionymus* species	Callionymidae
emerald shiner	*Notropis atherinoides*	Cyprinidae
European eel	*Anguilla anguilla*	Anguillidae
fantail darter	*Etheostoma flabellare*	Percidae
fathead minnow	*Pimephales promelas*	Cyprinidae
flannelmouth sucker	*Catostomus latipinnis*	Catostomidae
flathead catfish	*Pylodictis olivaris*	Ictaluridae
flathead chub	*Platygobio gracilis*	Cyprinidae
freshwater drum	*Aplodinotus grunniens*	Sciaenidae
Gila chub	*Gila intermedia*	Cyprinidae
golden shiner	*Notemigonus crysoleucas*	Cyprinidae
goldeye	*Hiodon alosoides*	Hiodontidae
goldfish	*Carassius auratus*	Cyprinidae
grass carp	*Ctenopharyngodon idella*	Cyprinidae
green sunfish	*Lepomis cyanellus*	Centrarchidae
gudgeon	*Gobio gobio*	Cyprinidae
humpback chub	*Gila cypha*	Cyprinidae
humpback whitefish	*Coregonus pidschian*	Salmonidae
lake chubsucker	*Erimyzon sucetta*	Cyprinidae
lake trout	*Salvelinus namaycush*	Salmonidae
largemouth bass	*Micropterus salmoides*	Centrarchidae
largescale stoneroller	*Campostoma oligolepis*	Cyprinidae
least cisco	*Coregonus sardinella*	Salmonidae
longnose dace	*Rhinichthys cataractae*	Cyprinidae

Appendix A. Concluded.

Common name	Scientific name	Family
longnose sucker	*Catostomus catostomus*	Catostomidae
mottled sculpin	*Cottus bairdi*	Cottidae
mountain whitefish	*Prosopium williamsoni*	Salmonidae
Mozambique tilapia	*Tilapia mossambica*	Cichlidae
mummichog	*Fundulus heteroclitus*	Cyprinodontidae
northern pike	*Esox lucius*	Esocidae
northern hog sucker	*Hypentelium nigricans*	Catostomidae
Pacific sardine	*Sardinops sagax*	Clupeidae
paddlefish	*Polyodon spathula*	Polyodontidae
pink salmon	*Oncorhynchus gorbuscha*	Salmonidae
plaice	*Pleuronectes platessa*	Pleuronectidae
powan	*Coregonus lavaretus*	Salmonidae
pumpkinseed	*Lepomis gibbosus*	Centrarchidae
rainbow trout (steelhead)	*Oncorhynchus mykiss*	Salmonidae
razorback sucker	*Xyrauchen texanus*	Catostomidae
red shiner	*Cyprinella lutrensis*	Cyprinidae
river carpsucker	*Carpiodes carpio*	Catostomidae
roach	*Rutilus rutilus*	Cyprinidae
rosyside dace	*Clinostomus funduloides*	Cyprinidae
round whitefish	*Prosopium cylindraceum*	Salmonidae
roundtail chub	*Gila robusta*	Cyprinidae
roussette (spotted dogfish?)	(*Scyliorhinus canicula*?)	Scyliorhinidae
ruffe	*Gymnocephalus cernuus*	Percidae
sauger	*Stizostedion canadense*	Percidae
seahorse	*Hippocampus* species	Syngnathidae
shorthead redhorse	*Moxostoma macrolepidotum*	Catostomidae
shovelnose sturgeon	*Scaphirhynchus platorynchus*	Acipenseridae
Siberian sturgeon	*Acipenser baeri*	Acipenseridae
sicklefin chub	*Macrhybopsis meeki*	Cyprinidae
skate	(*Raja* species?)	Rajidae
smallmouth bass	*Micropterus dolomieu*	Centrarchidae
sockeye salmon	*Oncorhynchus nerka*	Salmonidae
sole	*Solea vulgaris*	Soleidae
speckled dace	*Rhinichthys osculus*	Cyprinidae
striped bass	*Morone saxatilis*	Percichthyidae
sturgeon chub	*Macrhybopsis gelida*	Cyprinidae
tench	*Tinca tinca*	Cyprinidae
Tennessee shiner	*Notropis leuciodus*	Cyprinidae
threespine stickleback	*Gasterosteus aculeatus*	Gasterosteidae
topsmelt	*Atherinops affinis*	Atherinidae
vendace	*Coregonus albula*	Salmonidae
walleye	*Stizostedion vitreum*	Percidae
warpaint shiner	*Luxilus coccogenis*	Cyprinidae
westslope cutthroat trout	*Oncorhynchus clarki lewisi*	Salmonidae
white crappie	*Pomoxis annularis*	Centrarchidae
white sucker	*Catostomus commersoni*	Catostomidae
woundfin	*Plagopterus argentissimus*	Cyprinidae
yellow perch	*Perca flavescens*	Percidae
Yellowstone cutthroat trout	*Oncorhynchus clarki bouvieri*	Salmonidae
zander (pikeperch)	*Stizostedion lucioperca*	Percidae

Appendix B. Compendium of reported electrofishing mortalities and injuries by fish species and electrical current. Extracted from published literature, agency documents, personal communications, and, with permission, unpublished manuscripts.[a,b]

Species: Lengths (cm) or develop. intervals	Species: No. obs.	Adverse Effects: Delayed equil., recov.	Mortality: Short-term	Mortality: Long-term	Brands	Spinal Injuries: Spine/Vertebrae Extern.	Spinal Injuries: Spine/Vertebrae Intern.	Spinal Injuries: Intern. hemor.	Other injuries	Environment: Where fish were subjected to electric field	Conductivity (μS/cm)	Temp. (°C)	Electric Field and Current: Fd tp	Current type	Frequency (Hz)	Pulse duration (ms)	Waveform	Source (pc = pers. commun.) (um = unpubl. ms.)
Acipenseridae																		
Scaphirhynchus platorynchus, shovelnose sturgeon																		
≤91 TL	5						0%	0%		Rivers	600	11	*	PDC	60	8?	Sq.	Fredenberg 1992
≤77 TL	3						0%	0%		Rivers	600	11	*	CPS	240/15	2.6/11	Sq.	Fredenberg 1992
Polyodontidae																		
Polyodon spathula, paddlefish																		
			high[c]				high[c]			Rivers			*	PDC				Pfeifer pc
Hiodontidae																		
Hiodon alosoides, goldeye																		
11-37 TL	19		0%		0%		21%	21%		Rivers	351-425	12-15	*	DC[fy]				Grisak 1996
11-37 TL	23		0%		0%		4%	39%		Rivers	351-425	12-15	*	PDC[fy]	40	6.3	Sq.	Grisak 1996
Cyprinidae																		
Campostoma oligolepis, largescale stoneroller																		
	few		≥0%[dl]							Streams	10-15	5-8	*	DC				Barrett & Grossman'88
Carassius auratus, goldfish																		
6-9			0[d]		0[d]	0[d]			0[d]	Lab. trough	18-10000	20	=	AC	60		Sine	Kolz & Reynolds 1989
6-9			0[d]		0[d]	0[d]			0[d]	Lab. trough	9.5-10000	20	=	DC				Kolz & Reynolds 1989
6-9			0[d]		0[d]	0[d]			0[d]	Lab. trough	13-10000	20	=	PDC	50	10	Sq.	Kolz & Reynolds 1989
6-9			0[d]		0[d]	0[d]			0[d]	Lab. trough	13-9700	20	=	PDC	50	2	Sq.	Kolz & Reynolds 1989
12-15 TL	32		0%		0%					Aquarium			*	PDC	100	2.5	Sq.	Sorensen 1994
Clinostomus funduloides, rosyside dace																		
.	few		≥0%[dl]							Streams	10-15	5-8	*	DC				Barrett & Grossman'88
Cyprinella lutrensis, red shiner																		
	[e]				0	0				Rivers etc,CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
Cyprinus carpio, common carp																		
			1[f]			1[f]				Rivers, CRB			*	PDC				Kinsolving pc
			0		0	0				Rivers, CRB	500-800	15-25	*	PDC				Valdez pc
	[e]				0	0	0?			Rivers etc,CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
$\bar{x}$ =37 TL	39		0%				8%			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
45 TL	1		0				0			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
Gila cypha, humpback chub																		
			0			0				Rivers, CRB			*					Pfeifer pc
			~0.01%		X					Rivers, CRB	300-2000	5-25	*	PDC				Valdez pc
					X[g]				X[g]	Rivers etc,CRB			*	PDC				Trammell pc
					X[g]				X[g]	Rivers etc,CRB			*	CPS	240/15	2.6/11	Sq.	Trammell pc
5-10 TL	30		0%		0%	0%	0%	20%[h]		Test tank	940	15	=	CPS	240/15	2.6/11	Sq.	Ruppert & Muth 1997
Juv.-ad.			0		0					Rivers etc,CRB	250-3500		*	PDC,DC				Burdick pc
Gila elegans, bonytail																		
			~0.01%		0					Rivers, CRB	300-2000	5-25	*	PDC				Valdez pc

Appendix B. Continued.

Species		Adverse Effects								Environment			Electric Field and Current					Source
			Mortality		Spinal Injuries													
						Spine/Vertebrae												
Lengths (cm) or develop. intervals	No. obs.	Delayed equil., recov.	Short-term	Long-term	Brands	Extern.	Intern.	Intern. hemor.	Other injuries	Where fish were subjected to electric field	Conductivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Frequency (Hz)	Pulse duration (ms)	Wave-form	(pc = pers. commun.) (um = unpubl. ms.)
5-8 TL	90		0%		0%	0%	0%	3-20%[fp]		Test tank	940	15	=	PDC	30	4	Sq.	Ruppert & Muth 1997
5-8 TL	90		0%		0%	0%	0%	7-27%[fq]		Test tank	940	15	=	PDC	60	4	Sq.	Ruppert & Muth 1997
5-8 TL	90		0%		0%	0%	0%	13-23%[fr]		Test tank	940	15	=	PDC	80	5	Sq.	Ruppert & Muth 1997
5-8 TL	90		0%		0%	0%	0%	7-10%[fs]		Test tank	940	15	=	CPS	240/15	2.6/11	Sq.	Ruppert & Muth 1997
Gila robusta, roundtail chub																		
					0					Rivers, CRB	600-1000	15-20	*	PDC,DC?				Buntjer pc
			0		0	0				Rivers, CRB	500-800	15-25	*	PDC				Valdez pc
22-40 TL	40	0%	0%		0%	0%	0%	5%		River, CRB	1,000	20	*	PDC	40	5	Sq.	Cowdell & Valdez '94
	[c]				0	0				Rivers etc.CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
Luxilus coccogenis, warpaint shiner																		
	few		≥0%[dl]							Streams	10-15	5-8	*	DC				Barrett & Grossman'88
Luxilus cornutus, common shiner																		
5-9 TL	>16	X[em]	X[em]							Test tank			=	DC				Adams et al. 1972
Macrhybopsis gelida, sturgeon chub																		
Adult?	8[fz]		0%		0%		0%	0%		Bucket in River	351-425	12-15	*	PDC[fz]	40	6.3	Sq.	Grisak 1996
Macrhybopsis meeki, sicklefin chub																		
Adults?	9[fz]		0%		0%		0%	0%		Bucket in River	351-425	12-15	*	PDC[fz]	40	6.3	Sq.	Grisak 1996
Notemigonus crysoleucas, golden shiner																		
5-10 TL	7		0%[dx]							Lakes	>66, <520	13-14	*	AC	180[da]		[da]	Schneider 1992
Notropis leuciodus, Tennessee shiner																		
.	few		≥0%[dl]							Streams	10-15	5-8	*	DC				Barrett & Grossman'88
Pimephales promelas, fathead minnow																		
	[c]				0	0				Rivers etc.CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
Plagopterus argentissimus, woundfin																		
	[c]				0	0				Rivers etc.CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
Platygobio gracilis, flathead chub																		
11-24 TL	2		0%		0%		0%	0%		Rivers	351-425	12-15	*	DC[fy]				Grisak 1996
11-24 TL	12		0%		0%		8%	0%		Rivers	351-425	12-15	*	PDC[fy]	40	6.3	Sq.	Grisak 1996
Ptychocheilus lucius, Colorado pikeminnow																		
$\bar{x}$ = 33 TL	20		0		0	0	15%	5%		Test trough	530	18	=	DC[gi]				Meismer 1999
$\bar{x}$ = 34 TL	20		0		0	0	5%	0		Test trough	530	18	=	DC[gj]				Meismer 1999
$\bar{x}$ = 34 TL	20		0		0	0	5%	0		Test trough	530	18	=	DC[gk]				Meismer 1999
$\bar{x}$ = 34 TL	20		0		0	0	0	5%		Test trough	530	18	=	DC[gl]				Meismer 1999
			0			0				Rivers, CRB			*					Pfeifer pc
Juv.-ad.			0	low[k]	1[k]					Rivers etc.CRB	250-3500		*	PDC&DC				Burdick pc
					0					Rivers, CRB	600-1000	15-20	*	PDC,DC?				Buntjer pc
					X[l]					Rivers, CRB			*	PDC?				Hawkins pc
Juv.-ad.			1[j]						1[j]	Rivers etc.CRB			*	PDC			Sq.	Emblad pc

Appendix B. Continued.

Species		Adverse Effects								Environment				Electric Field and Current				Source
Lengths (cm) or develop. intervals	No. obs.	Delayed equil., recov.	Mortality: Short-term	Mortality: Long-term	Brands	Spinal Injuries: Spine/Vertebrae Extern.	Spinal Injuries: Spine/Vertebrae Intern.	Spinal Injuries: Intern. hemor.	Other injuries	Where fish were subjected to electric field	Conductivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Frequency (Hz)	Pulse duration (ms)	Waveform	(pc = pers. commun.) (um = unpubl. ms.)
10-90 TL		X[h]	0	low[h]	1[h]					Rivers, CRB	200-2000	0-25	*	PDC				McAda pc
			~0.01%		X					Rivers, CRB	300-2000	5-25	*	PDC				Valdez pc
Adults	20		0	5%?[i]	0	0				Rivers, CRB	300-1500	5-15	*	PDC	30,40	20		Valdez pc
$\bar{x}$ = 34 TL	20		0		0	0	15%	0		Test trough	530	18	=	PDC[gi]	15	4	Sq.	Meismer 1999
$\bar{x}$ = 33 TL	20		0		0	0	5%	0		Test trough	530	18	=	PDC[gj]	15	4	Sq.	Meismer 1999
$\bar{x}$ = 34 TL	20		0		0	0	10%	5%		Test trough	530	18	=	PDC[gk]	15	4	Sq.	Meismer 1999
$\bar{x}$ = 34 TL	20		0		0	0	15%	0		Test trough	530	18	=	PDC[gl]	15	4	Sq.	Meismer 1999
$\bar{x}$ = 34 TL	20		0		0	0	5%	0		Test trough	530	18	=	PDC[gi]	60	4	Sq.	Meismer 1999
$\bar{x}$ = 33 TL	20		0		0	0	0	0		Test trough	530	18	=	PDC[gj]	60	4	Sq.	Meismer 1999
$\bar{x}$ = 34 TL	20		0		0	0	0	5%		Test trough	530	18	=	PDC[gk]	60	4	Sq.	Meismer 1999
$\bar{x}$ = 34 TL	20	X[gn]	0		0	0	5%	0		Test trough	530	18	=	PDC[gl]	60	4	Sq.	Meismer 1999
$\bar{x}$ = 34 TL	20		0		0	0	0	0		Test trough	530	18	=	PDC[gm]	60	4	Sq.	Meismer 1999
$\bar{x}$ = 34 TL	20		0		0	0	0	0		Test trough	530	18	=	PDC[gm]	60	4	¼ Sine	Meismer 1999
$\bar{x}$ = 33 TL	20		0		0	0	10%	0		Test trough	530	18	=	CPS[gi]	240/15	2.6/11	Sq.	Meismer 1999
$\bar{x}$ = 33 TL	20		0		0	0	5%	0		Test trough	530	18	=	CPS[gj]	240/15	2.6/11	Sq.	Meismer 1999
$\bar{x}$ = 34 TL	20		0		0	0	5%	0		Test trough	530	18	=	CPS[gk]	240/15	2.6/11	Sq.	Meismer 1999
$\bar{x}$ = 33 TL	20		0		0	0	5%	5%		Test trough	530	18	=	CPS[gl]	240/15	2.6/11	Sq.	Meismer 1999
Rhinichthys cataractae, longnose dace																		
	few		≥0%[dl]							Streams	10-15	5-8	*	DC				Barrett & Grossman'88
Rhinichthys osculus, speckled dace																		
	[e]				0	0				Rivers etc,CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
Semotilus atromaculatus, creek chub																		
	few		≥0%[dl]							Streams	10-15	5-8	*	DC				Barrett & Grossman'88
Catostomidae *Carpiodes carpio*, river carpsucker																		
30-58 TL	4		0%		0%		0%	0%		Rivers	351-425	12-15	*	DC[fy]				Grisak 1996
30-58 TL	11		0%		0%		18%	9%		Rivers	351-425	12-15	*	PDC[fy]	40	6.3	Sq.	Grisak 1996
Catostomus catostomus, longnose sucker																		
~43-49TL	5		0%		0%		0%	0%		Rivers	351-425	12-15	*	PDC[fy]	40	6.3	Sq.	Grisak 1996
I+& older	229[ff]					7-13%				Stream (c)	34-63	<12-18	*	PDC	100	5	Sq.	Kocovsky et al. 1997
Catostomus catostomus, longnose sucker and *C. commersoni*, white sucker (combined data)																		
$\bar{x}$ = 41 TL	50						2%	16%		River	~450	10	*	DC				Fredenberg pc
$\bar{x}$ = 40 TL	52						2%	8%		River	~450	10	*	PDC	15		Sq.	Fredenberg pc
$\bar{x}$ = 39 TL	50						0%	4%		River	~450	10	*	CPS	240/15	2.6/11	Sq.	Fredenberg pc
Catostomus commersoni, white sucker																		
					X					Rivers, CRB			*	PDC?				Hawkins pc
			0		0	0				Rivers, CRB	500-800	15-25	*	PDC				Valdez pc
	[e]				0	0	0?			Rivers etc,CRB	<50->5000	>0->30	*	PDC	60			Krueger pc

Appendix B. Continued.

Species		Adverse Effects								Environment			Electric Field and Current					Source
			Mortality		Spinal Injuries													
						Spine/Vertebrae												
Lengths (cm) or develop. intervals	No. obs.	Delayed equil., recov.	Short-term	Long-term	Brands	Extern.	Intern.	Intern. hemor.	Other injuries	Where fish were subjected to electric field	Conductivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Frequency (Hz)	Pulse duration (ms)	Wave-form	(pc = pers. commun.) (um = unpubl. ms.)
37 TL	1		0				0			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
Catostomus discobolus, bluehead sucker																		
					0					Rivers, CRB	600-1000	15-20	*	PDC,DC?				Buntjer pc
					X					Rivers, CRB			*	PDC?				Hawkins pc
			~0.01%		X					Rivers, CRB	300-2000	5-25	*	PDC				Valdez pc
			0		0	0				Rivers, CRB	500-800	15-25	*	PDC				Valdez pc
	[c]				0	0	0?			Rivers etc,CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
Catostomus latipinnis, flannelmouth sucker																		
			~0.01%		X					Rivers, CRB	300-2000	5-25	*	PDC				Valdez pc
			0		0	0				Rivers, CRB	500-800	15-25	*	PDC				Valdez pc
	[c]				0	0	0?			Rivers etc.CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
					0					Rivers, CRB	600-1000	15-20	*	PDC,DC?				Buntjer pc
					X					Rivers, CRB			*	PDC?				Hawkins pc
Erimyzon sucetta, lake chubsucker																		
5-25 TL	41		0%[dv]							Lakes	>66, <520	13-14	*	AC	180[da]		[da]	Schneider 1992
Hypentelium nigricans, northern hog sucker																		
	few		≥0%[dl]							Streams	10-15	5-8	*	DC				Barrett & Grossman'88
Moxostoma macrolepidotum, shorthead redhorse																		
18-49 TL	4		0%		0%		0%	0%		Rivers	351-425	12-15	*	DC[f]				Grisak 1996
18-49 TL	20		0%		0%		0%	5%		Rivers	351-425	12-15	*	PDC[f]	40	6.3	Sq.	Grisak 1996
Xyrauchen texanus, razorback sucker																		
Juv.-ad.			0		0					Rivers etc, CRB	250-3500		*	PDC,DC				Burdick pc
	~50		0		0					Rivers, CRB	200-2000	0-25	*	PDC				McAda pc
			~0.01%		0					Rivers, CRB	300-2000	5-25	*	PDC				Valdez pc
Adults	20		0	10%?[m]	0	0				Rivers, CRB	300-1500	5-15	*	PDC	30,40	20		Valdez pc
0.9-1.0SL	60	0%	0%						0%[fo]	Test tank	650	19	=	PDC	30	4	Sq.	Muth & Ruppert 1997
0.9-1.0SL	180	100%[fo]	0%						0%[fo]	Test tank	650	19	=	PDC	60	4	Sq.	Muth & Ruppert 1997
50-60 TL	8				0%	0%	13%	50%	0%	Test tank	610	20	=	PDC	60	4	Sq.	Muth & Ruppert 1996
0.9-1.0SL	60	100%[fo]	0%						0%[fo]	Test tank	650	19	=	PDC	80	5	Sq.	Muth & Ruppert 1997
0.9-1.0SL	60	100%[fo]	0%						0%[fo]	Test tank	650	19	=	CPS	240/15	2.6/11	Sq.	Muth & Ruppert 1997
50-60 TL	7				0%	0%	0%	14%	0%	Test tank	610	20	=	CPS	240/15	2.6/11	Sq.	Muth & Ruppert 1996
Ictaluridae																		
Ictalurus punctatus, channel catfish																		
Adults?	10		0%				≥60%			Hatch. ponds	167		*	AC	180[da]		[da]	Spencer 1967a & b
		X[n]			0					Rivers, CRB	600-1000	15-20	*	PDC,DC?				Buntjer pc
		X[o]								Rivers, CRB			*	PDC?				Hawkins pc
	[c]				0	0				Rivers etc,CRB	<50->5000	>0->30	*	PDC	60			Krueger pc

Appendix B. Continued.

Species		Adverse Effects								Environment			Electric Field and Current					Source
			Mortality			Spinal Injuries												
						Spine/Vertebrae												
Lengths (cm) or develop. intervals	No. obs.	Delay-ed equil., recov.	Short-term	Long-term	Brands	Extern.	Intern.	Intern. hemor.	Other injuries	Where fish were subjected to electric field	Conduc-tivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Freq-uency (Hz)	Pulse dura-tion (ms)	Wave-form	(pc = pers. commun.) (um = unpubl. ms.)
Esocidae																		
Esox lucius, northern pike																		
13-19 SL	17	24%	0%		24%	X			?	Aquaria	200-230	12-14	=	AC[fj]	50		Sine	Walker et al. 1994
13-19 SL	18	17%	0%		?	X			33%	Aquaria	200-230	12-14	=	AC[fj]	50		Triang.	Walker et al. 1994
Juv.-ad.			0		0					Streams	25-200	5-15	*	PDC?				Valdez pc
52-68 FL	27						11%	0%		Test tank	158-188	11-15	=	PDC	30	16.7		Roach 1992
36-74 FL	60						5%			Test tank	109-132	11-16	=	PDC100V	30	16.7		Roach 1992
36-74 FL	60						10%			Test tank	109-132	11-16	=	PDC400V	30	16.7		Roach 1992
13-19 SL	18	0%	0%		0%	0%			0%	Aquaria	200-230	12-14	=	PDC[fj]	50	7.3		Walker et al. 1994
45-97 SL	311	0%	0%		0%	0%			0%	Test tank	410	11	=	PDC[fk]	50	7.3		Walker et al. 1994
36-74 FL	60						8%			Test tank	109-132	11-16	=	PDC100V	60	8.3		Roach 1992
36-74 FL	60						12%			Test tank	109-132	11-16	=	PDC400V	60	8.3		Roach 1992
52-68 FL	27						33%[av]	15%[av]		Test tank	158-188	11-15	=	PDC	60	8.3		Roach 1992
40->80FL	32		0.2%[as]	[at]			16%[au]	19%[au]		Rivers	210		*	PDC	60	8.3		Holmes et al. 1990
	[c]				0	0	0?			Rivers etc,CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
38-77 FL	140/172[ar]			0%[ar]			28%[ar]			Test tank	1017-1090	10-13	=	PDC	120	4.2		Roach 1992
Salmonidae (unspecified species)																		
Juv.-ad.			0				most[q]		X[q]	Rivers etc,CRB	250-3500		*	PDC,DC				Burdick pc
<46 TL						X[p]				Rivers, streams	<100		*	PDC				Gowan pc
10-24 TL	114[fh]						44%[fh]			Streams	34-63	<12-18	*	PDC	100	5	Sq.	Kocovsky et al. 1997
Coregonus pidschian, humpback whitefish																		
33-45	278/60		5%[r]				3%[s]	7%[s]		Rivers	80-88	10-11	*	PDC	80	5		Holmes et al. 1990
Coregonus sardinella, least cisco																		
28-38	106/83		15%[t]				5%[u]		30%[u]	Rivers	80-88	10-11	*	PDC	80	5		Holmes et al. 1990
Oncorhynchus clarki, cutthroat trout																		
			0.5%		10%					Streams	<100	5-15	*	DC?				Valdez pc
Yoy-ad					X[v]					Rivers, CRB	<25?-1000	0-19	*	PDC				Buntjer pc
[w]					<1%					Streams	10-100		*	DC?				Valdez pc
Oncorhynchus gorbuscha, pink salmon																		
Juv.-ad.		high		low[x]	high					Streams		5-15	*	AC	60			Valdez pc
Oncorhynchus kisutch, coho salmon																		
7 TL	107		78%[de]							Lab shock tank		17	=	PDC	8	40	Sq.	Collins et al. 1954
7 TL	107		0%[df]							Lab shock tank		17	=	PDC	8	40	Sq.	Collins et al. 1954
6-10 SL	197		3%[cy]							Hatch. raceway	67-100	17	*	PDC	15	8.3	½ Sine	Pugh 1962
6-10 SL	207		2%[cy]							Hatch. raceway	200-1000	17	*	PDC	15	8.3	½ Sine	Pugh 1962
6-10 SL	195		9%[cy]							Hatch. raceway	67-100	17	*	PDC	15	8.3	Sq.	Pugh 1962
6-10 SL	206		4%[cy]							Hatch. raceway	200-1000	17	*	PDC	15	8.3	Sq.	Pugh 1962
6-10 SL	194		7%[cy]							Hatch. raceway	67-100	17	*	PDC	30	8.3	½ Sine	Pugh 1962

Appendix B. Continued.

Species		Adverse Effects								Environment				Electric Field and Current				Source
Lengths (cm) or develop. intervals	No. obs.	Delayed equil., recov.	Mortality: Short-term	Mortality: Long-term	Spinal Injuries: Brands	Spinal Injuries: Spine/Vertebrae Extern.	Spinal Injuries: Spine/Vertebrae Intern.	Spinal Injuries: Intern. hemor.	Other injuries	Where fish were subjected to electric field	Conductivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Frequency (Hz)	Pulse duration (ms)	Waveform	(pc = pers. commun.) (um = unpubl. ms.)
6-10 SL	207		5%[cj]							Hatch. raceway	200-1000	17	*	PDC	30	8.3	½ Sine	Pugh 1962
6-10 SL	194		18%[cj]							Hatch. raceway	67-100	17	*	PDC	30	8.3	Sq.	Pugh 1962
6-10 SL	194		6%[cj]							Hatch. raceway	200-1000	17	*	PDC	30	8.3	Sq.	Pugh 1962
Oncorhynchus mykiss, rainbow trout																		
>40 FL	22						50%			Rivers	>50	>7	*					Reynolds et al. 1988
>40 FL							X[y]			Rivers,net-pens			*					Reynolds et al. 1988
~19 TL	48		4%[cw]							Hatch. raceway	306 @25C		*	AC				Pratt 1955
5-9.9 TL	45[fc]		15-23%				0%	0%		Stream	14	15	*	AC	60			Habera et al. 1996
10-23 TL	182[fd]		2-9%				0-10%	0-6%		Stream	14	15	*	AC	60			Habera et al. 1996
Large	503	X	26%		X	X	X	X	X[ci]	Canal		14-21	*	AC	60		Sine	Hauck 1949
11-27 TL	50						0%[cu]			Test tank	475-550	11-13	*	AC	60		Sine	McCrimmon & ... '65
4-36 SL	46		4%							Test tank	1494?	16-18	=	AC	60			Taylor et al. 1957
x̄ = 46 FL	12						58%	25%		Test tank	100-121	9-13	=	AC,100V	60		Sine	Taube 1992
x̄ = 48 FL	12						75%	58%		Test tank	100-121	9-13	=	AC,400V	60		Sine	Taube 1992
16-26	375		3%[dh]		2%[dh]		[di]			Hatch. raceway	10	6	*	AC,350V	300			Hudy 1985
16-26	375		2%[dh]		2%[dh]		[di]			Hatch. raceway	10	6	*	AC,700V	300			Hudy 1985
16-26	375		1%[dh]		1%[dh]		[di]			Hatch. raceway	10	6	*	AC,760V	250-300			Hudy 1985
4-36 SL	91		0%							Test tank	1494?	16-18	=	DC				Taylor et al. 1957
Large				~35%[ck]			<18%			Test tank			=	DC				Reynolds et al. 1992
x̄ = 46 FL	18						33%	28%		Test tank	100-121	9-13	=	DC,100V				Taube 1992
x̄ = 47 FL	18						22%	28%		Test tank	100-121	9-13	=	DC,400V				Taube 1992
x̄ = 40FL	12			0%[cs]			17%			Hatch. raceway	103	11	*	DC,200V				Taube 1992
x̄ = 32FL	18		11%				47%			Stream	30	7	*	DC				Taube 1992
x̄ = 34FL	33		3%				0%			Stream	30	7	*	DC				Taube 1992
~19 TL	48		2%[cx]							Hatch. raceway	306 @25C		*	DC				Pratt 1955
~20 TL	16		13%[ct]			6%				Hatchery		6-10	*	DC				Bouch and Ball 1966
~12	60		0-13%[dn]							Lab shock tank	<450[dn]	13-21	=	DC				Kynard & Lonsdale'75
~14-48FL	32/23[cl]		0%[cl]		3%[cl]		4%[cl]	4%[cl]		Hatch. raceway	80	9-11	*	DC,300V				McMichael 1993[cm]
~14-48FL	25/29[cl]		~3%[cl]		8%[cl]		14%[cl]	17%[cl]		Hatch. raceway	80	9-11	*	DC,400V				McMichael 1993[cm]
~15-39FL	241		5%[cr]			0%	12%			Rivers	260	13-16	*	DC				Dalbey et al. 1996
30-43 TL	56						13%[bk,bl]	25%[bk,bl]		Rivers	300-320	6-12	*	DC				Fredenberg 1992
25-47 TL	21						5%[bk]	0%[bk]		Rivers	177	10-15	*	DC				Fredenberg 1992
27-54 TL	28						18%[bk,bm]	11%[bk,bm]		Rivers	540	18	*	DC				Fredenberg 1992
x̄ = 39 TL	50						6%	2%		River	~450	10	*	DC				Fredenberg pc
x̄ = 31 TL	20		0		15%	0	0			Test trough	530	18	=	DC[gi]				Meismer 1999
x̄ = 31 TL	20		0		20%	0	0			Test trough	530	18	=	DC[gj]				Meismer 1999
x̄ = 32 TL	20		0		30%	0	0			Test trough	530	18	=	DC[gk]				Meismer 1999
x̄ = 30 TL	20		0		10%	0	10%			Test trough	530	18	=	DC[gl]				Meismer 1999
33-43 TL	47						30%[bk,bn]	72%[bk,bn]		Rivers	300-320	6-12	*	Hybrid[bz]	60	<8?	½ Sine	Fredenberg 1992

Appendix B. Continued.

Species		Adverse Effects								Environment			Electric Field and Current					Source
Lengths (cm) or develop. intervals	No. obs.	Delay-ed equil., recov.	Mortality: Short-term	Mortality: Long-term	Spinal Injuries: Brands	Spinal Injuries: Spine/Vertebrae Extern.	Spinal Injuries: Spine/Vertebrae Intern.	Spinal Injuries: Intern. hemor.	Other injuries	Where fish were subjected to electric field	Conduc-tivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Freq-uency (Hz)	Pulse dura-tion (ms)	Wave-form	(pc = pers. commun.) (um = unpubl. ms.)
~15-39FL	309		1%[cr]			1%	40%			Rivers	260	13-16	*	Hybrid[bz]	60		½ Sine	Dalbey et al. 1996
~20-55TL	152				26%[bx]		63%[bx]			Rivers	540-900	7-18	*	Various[bx]				Fredenberg 1992
Yoy-ad					X[v]					Rivers, CRB	<25?-1000	0-19	*	PDC				Buntjer pc
20-68 FL	72/32[z]		14%[aa]		24%		75%[ab]	75%[ab]		Rivers	70	6.3	*	PDC				Holmes et al. 1990
4-36 SL	1641		0.3%							Test tank	1494?	16-18	=	PDC		33%[bg]		Taylor et al. 1957
					X?[g]				X?[g]	Rivers etc, CRB			*	PDC				Trammell pc
			0		X	0				Rivers, CRB	500-800	15-25	*	PDC				Valdez pc
			~0.01%		X					Rivers, CRB	300-2000	5-25	*	PDC				Valdez pc
Juv, 19TL	825			7%?[bi]						Test tank	143-172	11-13	=[bi]	PDC	5	60	Sq.?[bi]	Maxfield et al. 1971
Yoy, 5TL	954[bj]			10%?[bj]						Test tank	114-132	9-11	=[bj]	PDC	8	40	Sq.?[bj]	Maxfield et al. 1971
>30 TL	38						3%			Rivers, CRB	600-800	9-11	*	PDC	15	4	Sq.	Sharber et al. 1994
Adults	40						3%[ac]			Lab. trough	572	12	=	PDC	15	5	Sq.	Sharber pc
x̄ = 38 TL	50						20%	22%		River	~450	10	*	PDC	15		Sq.	Fredenberg pc
x̄ = 31 TL	20		0		0	0	0			Test trough	530	18	=	PDC[gi]	15	4	Sq.	Meismer 1999
x̄ = 31 TL	20		0		0	0	0			Test trough	530	18	=	PDC[gj]	15	4	Sq.	Meismer 1999
x̄ = 31 TL	20		0		25%	0	5%			Test trough	530	18	=	PDC[gk]	15	4	Sq.	Meismer 1999
x̄ = 31 TL	20		0		40%	0	0			Test trough	530	18	=	PDC[gl]	15	4	Sq.	Meismer 1999
x̄ = 41 FL	12			25%[cs]			58%			Hatch. raceway	103	11	*	PDC200V	20	12.5	Sq.	Taube 1992
x̄ = 42 FL	12			17%[cs]			25%			Hatch. raceway	103	11	*	PDC200V	20	37.5	Sq.	Taube 1992
x̄ = 36FL	20		15%				57%			Stream	30	7	*	PDC	25	30	Sq	Taube 1992
>30 TL	38						24%			Rivers, CRB	600-800	9-11	*	PDC	30	4	Sq.	Sharber et al. 1994
~14-48FL	27/23[cl]		0%[cl]		4%[cl]		22%[cl]	35%[cl]		Hatch. raceway	80	9-11	*	PDC	30	4.2	Sq.	McMichael 1993[cm]
x̄ = 40 FL	12			25%[cs]			33%			Hatch. raceway	103	11	*	PDC200V	30	16.7	Sq.	Taube 1992
x̄ = 41 FL	12						58%	42%		Test tank	100-121	9-13	=	PDC100V	30	16.7	Sq	Taube 1992
x̄ = 39 FL	12						33%	50%		Test tank	100-121	9-13	=	PDC400V	30	16.7	Sq	Taube 1992
x̄ = 40 FL	12						42%	58%		Test tank	100-121	9-13	=	PDC100V	30	25	Sq	Taube 1992
x̄ = 40 FL	12						42%	33%		Test tank	100-121	9-13	=	PDC400V	30	25	Sq	Taube 1992
14-40 TL	34[ch]						35%[ch]			Rivers	340-350	7-8	*	PDC	40	5	Sq.?	WY Game Fish '91[cj]
16-31 TL	11[ci]						0%[ci]			Rivers	340-350	7-8	*	PDC	40	5	Sq.?	WY Game Fish '91[cj]
14-32	240/4[du]		1-3%[du]				0%[du]			River, scap net	<250?	11-12	*	PDC	45	1.6	Sq.	Shetter et al. 1969
28-61	75		0%[dv]							River, scap net	<250?	11-12	*	PDC	45	1.6	Sq.	Shetter et al. 1969
Large				~35%[ck]			<20-60%			Test tank			=	PDC	20-60			Reynolds et al. 1992
30-56 TL	99						44%	[ad]		Rivers, CRB	600-800	9-11	*	PDC	60	4.2	Expo.	Sharber & Carothers'88
30-56 TL	55						67%	[ad]		Rivers, CRB	600-800	9-11	*	PDC	60	4.2	¼ Sine	Sharber & Carothers'88
x̄ = 30 TL	20		0		50%	0	5%			Test trough	530	18	=	PDC[gm]	60	4	¼ Sine	Meismer 1999
26-43 TL	50[cc]		≤8%[cc]				60%			Rivers	299		*	PDC[cd]	60?[cd]	7[cd]	¼Sine?	Meyer & Miller 1990[ce]
30-36 TL	9		78%?[cf]				78%			Rivers	600-616		*	PDC[cf]	60	7	¼Sine?	Meyer & Miller 1990[ce]
~15-39FL	316		0.3%[cr]			2%	54%			Rivers	260	13-16	*	PDC	60	8	½ Sine	Dalbey et al. 1996
20-47 TL	50						18%	28%		Rivers	257	6	*	PDC[cu]	60	8	½ Sine	Thompson et al. 1997a

Appendix B. Continued.

Species		Adverse Effects								Environment			Electric Field and Current					Source
		Delayed	Mortality			Spinal Injuries												
						Spine/Vertebrae		Intern. hemor.										
Lengths (cm) or develop. intervals	No. obs.	equil., recov.	Short-term	Long-term	Brands	Extern.	Intern.		Other injuries	Where fish were subjected to electric field	Conductivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Frequency (Hz)	Pulse duration (ms)	Waveform	(pc = pers. commun.) (um = unpubl. ms.)
21-48 TL	51						55%	65%		Rivers	114	3	*	PDC[cv]	60	8	½ Sine	Thompson et al. 1997a
13-51 TL	53[cw]						64%	43%		Rivers	134	6	*	PDC[cw]	60	8	½ Sine	Thompson et al. 1997a
14-45 TL	48						6%	13%		Rivers	270	7	*	PDC[cx]	60	8	½ Sine	Thompson et al. 1997a
22-50 TL	43						40%	49%		Rivers	90	2-4	*	PDC[cy]	60	8	½ Sine	Thompson et al. 1997a
14-43 TL	52[cz]						22%	40%		Rivers	145	1-5	*	PDC[cz]	60	8	½ Sine	Thompson et al. 1997a
Adults?[cn]			≤0.5%							Streams	<100-200	<10-15	*	PDC[co]	60?[co]	8[co]	½ Sine	Nehring 1991
Adults?[cn]			<1-5%			<1-5%				Streams	<100-200	<10-15	*	PDC[cp]	60?[cp]	8[cp]	½ Sine	Nehring 1991
24-45 TL	39[bu]						59%[bk,bu]	87%[bk,bu]		Rivers	33-55	4-6	*	PDC	60	8	½ Sine	Fredenberg 1992
24-48 TL	23						52%[bk,bv]	61%[bk,bv]		Rivers	150-175	13	*	PDC	60	8	½ Sine	Fredenberg 1992
31-43 TL	45						42%[bk,bt]	69%[bk,bt]		Rivers	300-320	6-12	*	PDC	60	~16	½ Sine	Fredenberg 1992
23-53 TL	54						50%[bk,bn]	59%[bk,bn]		Rivers	880-900	7-11	*	PDC?[bn]	60?[bn]	8?[bn]	Sq.?[bn]	Fredenberg 1992
x̄ = 30 TL	20		0		0	0	0			Test trough	530	18	=	PDC[gi]	60	4	Sq.	Meismer 1999
x̄ = 30 TL	20		0		45%	0	5%			Test trough	530	18	=	PDC[gj]	60	4	Sq.	Meismer 1999
x̄ = 30 TL	20		0		65%	0	0			Test trough	530	18	=	PDC[gk]	60	4	Sq.	Meismer 1999
x̄ = 30 TL	20	X[gn]	10%		75%	0	0			Test trough	530	18	=	PDC[gl]	60	4	Sq.	Meismer 1999
x̄ = 31 TL	20		30%		95%	0	15%			Test trough	530	18	=	PDC[gm]	60	4	Sq.	Meismer 1999
>30 TL	116						43%			Rivers, CRB	600-800	9-11	*	PDC	60	4	Sq.	Sharber et al. 1994
>30 TL	60						43%			Rivers, CRB	600-800	9-11	*	PDC	60	4	Sq.	Sharber et al. 1994
>30 TL	23						65%			Rivers, CRB	600-800	9-11	*	PDC	60	4	Sq.	Sharber et al. 1994
Adults							33%[ae]			Lab. trough[ae]	572?	12?	=	PDC	60	4	Sq.	Sharber pc
Adults							3%[af]			Lab. trough[af]	572?	12?	=	PDC	60	4	Sq.	Sharber pc
Adults	30						18%			Hatch. raceway				PDC	60	4.2	Sq.	Sharber pc
30-56 TL	55						44%	[ad]		Rivers, CRB	600-800	9-11	*	PDC	60	4.2	Sq.	Sharber & Carothers'88
41-52 TL	30						13%[bk]	57%[bk]		Streams	195	6	*	PDC	60	8?	Sq.	Fredenberg 1992
30-43 TL	42[bo]						67%[bk,bo]	91%[bk,bo]		Rivers	33-34	4-6	*	PDC	60	8?	Sq.	Fredenberg 1992
26-53 TL	46						68%[bk,bp]	59%[bk,bp]		Rivers	880-900	7-11	*	PDC	60	8?	Sq.	Fredenberg 1992
x̄ = 48 FL	12						58%	50%		Test tank	100-121	9-13	=	PDC100V	60	8.3	Sq	Taube 1992
x̄ = 46 FL	12						42%	33%		Test tank	100-121	9-13	=	PDC400V	60	8.3	Sq	Taube 1992
x̄ = 39 FL	12			8%[cs]			67%			Hatch. raceway	103	11	*	PDC200V	60	8.3	Sq.	Taube 1992
x̄ = 39 FL	102			35%[ct]			25%			Test tank	95-104	10-12	*	PDC250V	60	8.3	Sq.	Taube 1992
15-35 TL	628[fa]		8.5%				70%			Test tank	283	10-12	=	PDC150V	60		Sq.	Zeigenfuss 1995
17-35 TL	184[fb]		1.7%				41%			Test tank	226	8	=	PDC300V	60		Sq.	Zeigenfuss 1995
(30-120g)	120		0%[fv]							Test tank	240-270	15-20	=	PDC200V	60	5		Mitton & McDonald94
(50-600g)	15						0%			Test tank	240-270	7	=	PDC200V	60	5		Mitton & McDonald94
(~100g)	5						0%			Test tank	240-270	7	=	PDC400V	60	5		Mitton & McDonald94
(50,100g)	30						0%			Test tank	240-270	7	=	PDC600V	60	5		Mitton & McDonald94
(~600g)	15						10-20%			Test tank	240-270	7	=	PDC600V	60	5		Mitton & McDonald94
19-20 TL	102			2%?[bh]	39%[bh]					Hatch. raceway	242 @ 25C		*	PDC	60			Horak & Klein 1967
~35			0			1[ac]				Rivers, CRB			*	PDC	60			Kinsolving pc
Adults?	[c]				50%	0?	50%?			Rivers etc.CRB	<50->5000	>0->30	*	PDC	60			Krueger pc

Appendix B. Continued.

Species: Lengths (cm) or develop. intervals	Species: No. obs.	Adverse Effects: Delayed equil., recov.	Mortality: Short-term	Mortality: Long-term	Brands	Spinal Injuries: Spine/Vertebrae Extern.	Spinal Injuries: Spine/Vertebrae Intern.	Spinal Injuries: Intern. hemor.	Other injuries	Environment: Where fish were subjected to electric field	Conductivity (µS/cm)	Temp. (°C)	Fd tp	Electric Field and Current: Current type	Frequency (Hz)	Pulse duration (ms)	Waveform	Source (pc = pers. commun.) (um = unpubl. ms.)
~14-48FL	26/17[cl]		~0%[cl]		58%[cl]		35%[cl]	53%[cl]		Hatch. raceway	80	9-11	*	PDC	90	1.4	Sq	McMichael 1993[cm]
I+& older	1,014[ff]					2-6%				Stream (c)	34-63	<12-18	*	PDC	100	5	Sq.	Kocovsky et al. 1997
13-26 TL	30						0% [cu]			Test tank	500-550	11	*	PDC	120	8	½ Sine	McCrimmon & ... '65
28-37 TL	44						5-29%[bk]			Hatchery	238	4	*	PDC	250		Sq.	Fredenberg 1992
~33 TL	50/44[cp]		8%[cp]	0%[cp]		0%[cp]	0%[cp]	0%[cp]		Test tank	270-340	8	0	PDC[cq]	250	4?	½ Sine?	Dwyer & White 1995
>30 TL	37						62%			Rivers, CRB	600-800	9-11	*	PDC	512	0.2	Sq.	Sharber et al. 1994
>30 TL	43						9%			Rivers, CRB	600-800	9-11	*	CPS	240/15	2.6/11	Sq.	Sharber et al. 1994, pc
>30 TL	41						7%			Rivers, CRB	600-800	9-11	*	CPS	240/15	2.6/11	Sq.	Sharber et al. 1994, pc
Adults	30						6%			Hatch. raceway				CPS	240/15	2.6/11	Sq.	Sharber pc
x̄ = 31 TL	20		0		0	0	15%			Test trough	530	18	=	CPS[gi]	240/15	2.6/11	Sq.	Meismer 1999
x̄ = 31 TL	20		0		10%	0	0			Test trough	530	18	=	CPS[gj]	240/15	2.6/11	Sq.	Meismer 1999
x̄ = 31 TL	20		0		15%	0	0			Test trough	530	18	=	CPS[gk]	240/15	2.6/11	Sq.	Meismer 1999
x̄ = 30 TL	20		0		60%	0	5%			Test trough	530	18	=	CPS[gl]	240/15	2.6/11	Sq.	Meismer 1999
30-41 TL	4		[cg]				50%			Rivers	600-616		*	CPS	240/15	2.6/11	Sq.	Meyer & Miller 1990[ce]
16-39 TL	51[ci]						12%			Rivers	340-350	7-8	*	CPS	240/15	2.6/11	Sq.	WY Game Fish '91[cj]
40-50 TL	30						10%[bk]	77%[bk]		Streams	195	6	*	CPS	240/15	2.6/11	Sq.	Fredenberg 1992
30-43 TL	12[bq]						17%[bk]	25%[bk]		Rivers	35-55	4-6	*	CPS	240/15	2.6/11	Sq.	Fredenberg 1992
20-55 TL	44						43%[bk,br]	34%[bk,br]		Rivers	540	18	*	CPS	240/15	2.6/11	Sq.	Fredenberg 1992
23-43 TL	26						4%[bk,bs]	27%[bk,bs]		Rivers	158	10-12	*	CPS	240/15	2.6/11	Sq.	Fredenberg 1992
x̄ = 38 TL	50						2%	4%		River	~450	10	*	CPS	240/15	2.6/11	Sq.	Fredenberg pc
Large				~35%[ck]			<18%			Test tank			=	CPS	240/15	2.6/11	Sq.	Reynolds et al. 1992
x̄ = 41 FL	12						17%	33%		Test tank	100-121	9-13	=	CPS 100V	240/15	2.6/11	Sq	Taube 1992
x̄ = 39 FL	12						25%	50%		Test tank	100-121	9-13	=	CPS 400V	240/15	2.6/11	Sq	Taube 1992
x̄ = 38 FL	12			8%[cs]			8%			Hatch. raceway	103	11	*	CPS 200V	240/15	2.6/11	Sq.	Taube 1992
x̄ = 40 FL	8		0%				13%			Stream	30	7	*	CPS	240/15	2.6/11	Sq.	Taube 1992
Adults							8%[fl]			Anesthesia tank			*	CPS	240/15	2.6/11	Sq.	Tipping & Gihuly '96
Adults	1,015		0%[fm]							Anesthesia tank		4.5	*	CPS	240/15	2.6/11	Sq.	Tipping & Gihuly '96
Adults?					X?[g]				X?[g]	Rivers etc.CRB			*	CPS	240/15	2.6/11	Sq.	Trammell pc
Oncorhynchus tshawytscha, chinook salmon																		
x̄ = 7.9FL	~90		0%							Lab test tank	39[ga]	12	=	AC[gb]	60	20	Sine	McMillan 1928
x̄ = 7.9FL	~60		10%							Lab test tank	39[ga]	12	=	AC[gc]	60	20	Sine	McMillan 1928
x̄ = 7.9FL	~30		39%							Lab test tank	39[ga]	12	=	AC[gd]	60	20	Sine	McMillan 1928
x̄ = 7.9FL	~30		57%							Lab test tank	39[ga]	12	=	AC[ge]	60	20	Sine	McMillan 1928
x̄ = 7.9FL	~90		0%							Lab test tank	39[ga]	12	=	AC[gf]	60	20	Sine	McMillan 1928
x̄ = 7.9FL	~60		62-69%							Lab test tank	39[ga]	12	=	AC[gg]	60	20	Sine	McMillan 1928
x̄ = 7.9FL	~60		67-79%							Lab test tank	39[ga]	12	=	AC[gh]	60	20	Sine	McMillan 1928
Yoy, 7 TL	1843		0-77%[dm]							Lab shock tank	~50	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
Yoy, 7 TL	499		2-59%[dn]							Lab shock tank	50 & 85	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
4-6 TL	1441	X[do]	0-57%[do]							Lab shock tank	~48	10-20	=	PDC	2	20	Sq.	Collins et al. 1954

Appendix B. Continued.

Species		Adverse Effects								Environment			Electric Field and Current					Source
Lengths (cm) or develop. intervals	No. obs.	Delay-ed equil., recov.	Mortality		Spinal Injuries				Other injuries	Where fish were subjected to electric field	Conduc-tivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Freq-uency (Hz)	Pulse dura-tion (ms)	Wave-form	(pc = pers. commun.) (um = unpubl. ms.)
			Short-term	Long-term	Brands	Spine/Vertebrae Extern.	Spine/Vertebrae Intern.	Intern. hemor.										
6-8 TL	889	X[do]	1-78%[do]							Lab shock tank	~48	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
8-10 TL	201	X[do]	6-63%[do]							Lab shock tank	~48	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
10-12 TL	269	X[do]	5-58%[do]							Lab shock tank	~48	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
4-10 TL	168		0-1%[dp]							Lab shock tank	43	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
4-12 TL	323		0-7%[dp]							Lab shock tank	55	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
4-12 TL	269		0-15%[dp]							Lab shock tank	83	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
6-10 TL	123		9-10%[dp]							Lab shock tank	133	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
4-12 TL	215		0-13%[dp]							Lab shock tank	180	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
4-12 TL	242		4-58%[dp]							Lab shock tank	283	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
4-12 TL	52		8-75%[dp]							Lab shock tank	483	10-20	=	PDC	2	20	Sq.	Collins et al. 1954
4-10 TL	93		0%[dp]							Lab shock tank	53	20-25	=	PDC	2	20	Sq.	Collins et al. 1954
4-12 TL	115		0-18%[dp]							Lab shock tank	68	20-25	=	PDC	2	20	Sq.	Collins et al. 1954
4-8 TL	83		0-3%[dp]							Lab shock tank	78	20-25	=	PDC	2	20	Sq.	Collins et al. 1954
4-12 TL	454		0-18%[dp]							Lab shock tank	103	20-25	=	PDC	2	20	Sq.	Collins et al. 1954
4-12 TL	283		4-28%[dp]							Lab shock tank	128	20-25	=	PDC	2	20	Sq.	Collins et al. 1954
4-12 TL	204		10-44%	[dp]						Lab shock tank	195	20-25	=	PDC	2	20	Sq.	Collins et al. 1954
4-12 TL	174		15-59%	[dp]						Lab shock tank	303	20-25	=	PDC	2	20	Sq.	Collins et al. 1954
4-10 TL	105		49-67%	[dp]						Lab shock tank	483	20-25	=	PDC	2	20	Sq.	Collins et al. 1954
4-6 TL	315		0-26%[dq]							Lab shock tank	~50?	14	=	PDC	2	20	Sq.	Collins et al. 1954
6-8 TL	449		0-53%[dq]							Lab shock tank	~50?	14	=	PDC	2	20	Sq.	Collins et al. 1954
8-10 TL	154		0-50%[dq]							Lab shock tank	~50?	14	=	PDC	2	20	Sq.	Collins et al. 1954
4-6 TL	132		0-55%[dq]							Lab shock tank	~50?	18	=	PDC	2	20	Sq.	Collins et al. 1954
6-8 TL	678		6-52%[dq]							Lab shock tank	~50?	18	=	PDC	2	20	Sq.	Collins et al. 1954
8-10 TL	294		10-80%	[dq]						Lab shock tank	~50?	18	=	PDC	2	20	Sq.	Collins et al. 1954
9 TL	446		4-58%[dr]							Lab shock tank	45-65	12-20	=	PDC	2	20	Sq.	Collins et al. 1954
9 TL	412		0-38%[dr]							Lab shock tank	45-65	12-20	=	PDC	8	20	Sq.	Collins et al. 1954
9 TL	260		0-53%[ds]							Lab shock tank	50	10-16	=	PDC	8	20	Sq.	Collins et al. 1954
9 TL	192		4-38%[ds]							Lab shock tank	50	10-16	=	PDC	8	80	Sq.	Collins et al. 1954
4-6 TL	502		0-4%[dt]							Lab shock tank	38-68	10-20	=	PDC	3-8	20	Sq.	Collins et al. 1954
6-8 TL	317		3-6%[dt]							Lab shock tank	38-68	10-20	=	PDC	3-8	20	Sq.	Collins et al. 1954
8-10 TL	82		8-50%[dt]							Lab shock tank	38-68	10-20	=	PDC	3-8	20	Sq.	Collins et al. 1954
10-12 TL	46		6-50%[dt]							Lab shock tank	38-68	10-20	=	PDC	3-8	20	Sq.	Collins et al. 1954
4-6 TL	489		9-29%[dt]							Lab shock tank	38-68	10-20	=	PDC	10-15	20	Sq.	Collins et al. 1954
6-8 TL	548		0-28%[dt]							Lab shock tank	38-68	10-20	=	PDC	10-15	20	Sq.	Collins et al. 1954
8-10 TL	89		48-71%	[dt]						Lab shock tank	38-68	10-20	=	PDC	10-15	20	Sq.	Collins et al. 1954
10-12 TL	27		73-75%	[dt]						Lab shock tank	38-68	10-20	=	PDC	10-15	20	Sq.	Collins et al. 1954
$\bar{x}$ = 9 FL	71		16-25%							Circular tank	73	13	*	PDC500V	120		.	Maule & Mesa 1994
Prosopium cylindraceum, round whitefish																		
Juv.-ad.			0		X					Streams	25-200	5-15	*	PDC?				Valdez pc

Appendix B. Continued.

Species		Adverse Effects								Environment			Electric Field and Current					Source
Lengths (cm) or develop. intervals	No. obs.	Delay-ed equil., recov.	Mortality		Spinal Injuries				Other injuries	Where fish were subjected to electric field	Conduc-tivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Freq-uency (Hz)	Pulse dura-tion (ms)	Wave-form	(pc = pers. commun.) (um = unpubl. ms.)
			Short-term	Long-term	Brands	Spine/Vertebrae Extern.	Spine/Vertebrae Intern.	Intern. hemor.										
Prosopium williamsoni, mountain whitefish																		
									X[co]	Rivers			*	all				Fredenberg pc
x̄ = 36 TL	51						0%	6%		River	~450	10	*	DC				Fredenberg pc
x̄ = 35 TL	50						2%	18%		River	~450	10	*	PDC	15		Sq.	Fredenberg pc
x̄ = 36 TL	50						0%	2%		River	~450	10	*	CPS	240/15	2.6/11	Sq.	Fredenberg pc
Salmo trutta, brown trout																		
5-30			~0[ag]							Stream (box)			*					Chmielewski et al. '73
~19 TL	40		20%[cw]							Hatch. raceway	306 @25C		*	AC				Pratt 1955
~19 TL	49		4%[cx]							Hatch. raceway	306 @25C		*	DC				Pratt 1955
[ch]	20		0-6%[ch]							Stream, dip net			*	DC,500V				Lamarque '67a&b, '90
[ch]	20		0-17%[ch]							Stream, dip net			*	DC,400V	[ci]	.		Lamarque '67a&b, '90
30-51 TL	50						8%[by]	6%[by]		Rivers	300	6-12	*	DC				Fredenberg 1992
31-45 TL	50						32%[ca]	28%[ca]		Rivers	300	6-12	*	Hybrid[bz]	60	<8?	½ Sine	Fredenberg 1992
Yoy-ad					X[c]					Rivers, CRB	<25?-1000	0-19	*	PDC				Buntjer pc
			~0.01%		X					Rivers, CRB	300-2000	5-25	*	PDC				Valdez pc
			0		X	0				Rivers, CRB	500-800	15-25	*	PDC				Valdez pc
[ch]	20		0-86%[ch]							Stream, dip net			*	PDC		[cj]	Expo.	Lamarque '67a&b, '90
[ch]	20		0-93%[ch]							Stream, dip net			*	PDC		[ck]	Expo.	Lamarque '67a&b, '90
[ch]	20		0-50%[ch]							Stream, dip net			*	PDC[cl]	5	66	Sq.	Lamarque '67a&b, '90
17-38 TL	31[ch]						26%[ch]			Rivers	340-350	7-8	*	PDC	40	5	Sq.?	WY Game Fish '91[cj]
17-41 TL	34[ci]						15%[ci]			Rivers	340-350	7-8	*	PDC	40	5	Sq.?	WY Game Fish '91[cj]
	[e]				50%	0?	50%?			Rivers etc,CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
Adults?[cn]			≤0.5%							Streams	<100-200	<10-15	*	PDC[co]	60[co]	8[co]	½ Sine	Nehring 1991
Adults?[cn]			<1-5%			<1-5%				Streams	<100-200	<10-15	*	PDC[cp]	60[cp]	8[cp]	½ Sine	Nehring 1991
17-39 TL	56[cu]						25%	30%		Rivers	257	6	*	PDC[cu]	60	8	½ Sine	Thompson et al. 1997a
20-39 TL	33						18%	24%		Rivers	114	3	*	PDC[cv]	60	8	½ Sine	Thompson et al. 1997a
17-49 TL	64						52%	45%		Rivers	134	6	*	PDC[cw]	60	8	½ Sine	Thompson et al. 1997a
10-43 TL	56[cx]						27%	30%		Rivers	270	7	*	PDC[cx]	60	8	½ Sine	Thompson et al. 1997a
10-40 TL	55[cy]						31%	13%		Rivers	90	2-4	*	PDC[cy]	60	8	½ Sine	Thompson et al. 1997a
14-42 TL	53						38%	28%		Rivers	145	1-5	*	PDC[cz]	60	8	½ Sine	Thompson et al. 1997a
30-56 TL	50						36%[cb]	56%[cb]		Rivers	300	6-12	*	PDC	60	16	½ Sine	Fredenberg 1992
17-51 TL	28[cc]		≤4%[cc]				86%			Rivers	299		*	PDC[cd]	60?[cd]	7[d]	¼Sine?	Meyer & Miller 1990[ce]
28-54 TL	17		35%?[cf]				82%			Rivers	600-616		*	PDC	60	7	¼Sine?	Meyer & Miller 1990[ce]
[ch]	20		27-89%	[ch]						Stream, dip net			*	PDC[cm]	90	~11	½ Sine	Lamarque '67a&b, '90
1+& older	1,600[ff]					3-12%				Stream (c)	34-63	<12-18	*	PDC	100	5	Sq.	Kocovsky et al. 1997
13-59 TL	8		[cg]				25%			Rivers	600-616		*	CPS	240/15	2.6/11	Sq.	Meyer & Miller 1990[ce]
16-39 TL	59[ci]						14%			Rivers	340-350	7-8	*	CPS	240/15	2.6/11	Sq.	WY Game Fish '91[cj]
Salvelinus confluentus, bull trout																		
x̄ = 18	50		0%[fu]		0%[fu]					Test tank	219	9	=	DC,130V				Barton & Dwyer 1997

Appendix B. Continued.

Species		Adverse Effects								Environment			Electric Field and Current					Source
		Delay-ed equil., recov.	Mortality			Spinal Injuries												
						Spine/Vertebrae												
Lengths (cm) or develop. intervals	No. obs.		Short-term	Long-term	Brands	Extern.	Intern.	Intern. hemor.	Other injuries	Where fish were subjected to electric field	Conduc-tivity (µS/cm)	Temp. (°C)	Fd tp	Current type	Freq-uency (Hz)	Pulse dura-tion (ms)	Wave-form	(pc = pers. commun.) (um = unpubl. ms.)
Juv.-ad.			0		X[ah]					Streams	25-200	5-15	*	PDC?				Valdez pc
x̄ = 18	50		0%[fu]		0%[fu]					Test tank	219	9	=	PDC145V	60			Barton & Dwyer 1997
x̄ = 18	50		100%							Test tank	219	9	=	PDC293V	60			Barton & Dwyer 1997
Salvelinus fontinalis, brook trout																		
?9-24TL[cq]	70						13%[cr]	6%[cr]		Stream	440	11	*	AC.125V	250-300		2peaks	Hollender &Carline'94
?9-24TL[cq]	78						28%[cr]	19%[cr]		Stream	64	11	*	AC.350V	250-300		2peaks	Hollender &Carline'94
?9-24TL[cq]	65						9%[cr]	8%[cr]		Stream	50	10	*	AC.350V	250-300		2peaks	Hollender &Carline'94
?9-24TL[cq]	68						21%[cr]	18%[cr]		Stream	43	8	*	AC.400V	250-300		2peaks	Hollender &Carline'94
9-12 TL	117						16%			Streams	43-64, 440	8-11	*	AC	250-300		2peaks	Hollender &Carline'94
13-17 TL	130						32%			Streams	43-64, 440	8-11	*	AC	250-300		2peaks	Hollender &Carline'94
18-24 TL	34						41%			Streams	43-64, 440	8-11	*	AC	250-300		2peaks	Hollender &Carline'94
~25 TL	47		11%[cv]							Hatch. raceway	306 @25C		*	AC				Pratt 1955
12-24	375		0.5%[dh]		2%[dh]		di			Hatch. raceway	10	6	*	AC.350V	300			Hudy 1985
12-24	375		0.2%[dh]		2%[dh]		di			Hatch. raceway	10	6	*	AC.700V	300			Hudy 1985
12-24	375		0.2%[dh]		1%[dh]		di			Hatch. raceway	10	6	*	AC.760V	250-300			Hudy 1985
~25 TL	50		0%[cv]							Hatch. raceway	306 @25C		*	DC				Pratt 1955
Juv.-ad.			0		X					Streams	25-200	5-15	*	PDC?				Valdez pc
Yoy-ad					X[v]					Rivers, CRB	<25?-1000	0-19	*	PDC				Buntjer pc
?9-24TL[cq]	68						3%[cr]	7%[cr]		Stream	440	11	*	PDC200V	60		Sq.	Hollender &Carline'94
?9-24TL[cq]	95						26%[cr]	21%[cr]		Stream	64	11	*	PDC400V	60		Sq.	Hollender &Carline'94
?9-24TL[cq]	72						8%[cr]	10%[cr]		Stream	50	10	*	PDC500V	60		Sq.	Hollender &Carline'94
?9-24TL[cq]	63						11%[cr]	10%[cr]		Stream	43	8	*	PDC500V	60		Sq.	Hollender &Carline'94
9-12 TL	128						12%			Streams	43-64, 440	8-11	*	PDC	60		Sq.	Hollender &Carline'94
13-17 TL	128						26%			Streams	43-64, 440	8-11	*	PDC	60		Sq.	Hollender &Carline'94
18-24 TL	42						43%			Streams	43-64, 440	8-11	*	PDC	60		Sq.	Hollender &Carline'94
I+& older	731[ff]					5-14%				Stream (a)	34-63	<12-18	*	PDC	100	5	Sq.	Kocovsky et al. 1997
I+& older	360[fg]					0-2%				Stream (a)	34-63	<12-18	*	PDC	100	5	Sq.	Kocovsky et al. 1997
I+& older	1,304[ff]					4-23%				Stream (b)	34-63	<12-18	*	PDC	100	5	Sq.	Kocovsky et al. 1997
I+& older	275[fg]					0-3%				Stream (b)	34-63	<12-18	*	PDC	100	5	Sq.	Kocovsky et al. 1997
I+& older	2,544[ff]					2-6%				Stream (c)	34-63	<12-18	*	PDC	100	5	Sq.	Kocovsky et al. 1997
I+& older	2,122		0.5%							Streams			*	PDC	100[fi]	5[fi]	Sq.	Riley et al. 1992
Salvelinus malma, Dolly Varden																		
Juv.-ad.		high		low[x]	high					Streams		5-15	*	AC	60			Valdez pc
Salvelinus namaycush, lake trout																		
Adults[bf]			0		0	0				Lakes		1-5	*	PDC				Valdez pc
Thymallus arcticus, Arctic grayling																		
37-45 TL	25						0%	0%		Streams	33	6	*	DC				Fredenberg 1992
39-43 TL	25						0%	4%		Streams	33	6	*	Hybrid[bz]	60	<8?	½ Sine	Fredenberg 1992
Juv.-ad.			0		X					Streams	25-200	5-15	*	PDC?				Valdez pc

Appendix B. Continued.

Species: Lengths (cm) or develop. intervals	Species: No. obs.	Adverse Effects: Delayed equil., recov.	Mortality: Short-term	Mortality: Long-term	Brands	Spinal Injuries: Spine/Vertebrae Extern.	Spinal Injuries: Spine/Vertebrae Intern.	Spinal Injuries: Intern. hemor.	Other injuries	Environment: Where fish were subjected to electric field	Conductivity (μS/cm)	Temp. (°C)	Electric Field and Current: Fd tp	Current type	Frequency (Hz)	Pulse duration (ms)	Waveform	Source (pc = pers. commun.) (um = unpubl. ms.)
12-37 FL	88		3%[ai]		16%[aj]	5%	63%[ak]	27%[ak]		Rivers	60-88	9-15	*	PDC	40-120	3.3-10		Holmes et al. 1990
23-39 FL	616/60[z]		1%(+?)[al]		27%[am]		62%[an]	25%[an]		Rivers	39-40	9-11	*	PDC	80	5		Holmes et al. 1990
20-41 FL				~0% [ao]						Rivers, lakes	>39	8-11	*	PDC	80	5		Holmes et al. 1990
20-32 FL	103/60[z]		4%[ap]		0%		0-3%[aq]	5%[aq]		Rivers	80-88	10-11	*	PDC	80	5		Holmes et al. 1990
Gadidae																		
Lota lota, burbot																		
3-30?			<25->50%[go]							Lakes, littoral	37-61	2-18	*	DC				Eloranta 1990
Juv.-ad.			0		0					Streams	25-200	5-15	*	PDC?				Valdez pc
Gasterosteidae																		
Gasterosteus aculeatus, threespine stickleback																		
Juv.-ad.		high		low[x]	high					Streams		5-15	*	AC	60			Valdez pc
Cottidae (unspecified species)																		
		often[ax]	often[ax]							Riffles	<100		*	PDC				Gowan pc
Cottus bairdi, mottled sculpin																		
3-9 SL	90		0-3%[dj]							Streams	10-15	5-8	*	DC				Barrett & Grossman'88
4-9 SL	~57		0-12%[dj]							Streams	10-15	14-16	*	DC				Barrett & Grossman'88
4-8 SL	50		35-60%[dk]							Exp. channel		12-14	*	DC				Barrett & Grossman'88
Centrarchidae																		
Lepomis cyanellus, green sunfish																		
7-13 TL	51		10% [dy]							Ponds	>66, <520	0-4	*	AC	180[da]		[da]	Schneider 1992
Lepomis gibbosus, pumpkinseed																		
6-20 TL	174		0-1%[dz]							Lakes	>66, <520	13-28	*	AC	180[da]		[da]	Schneider 1992
67-20 TL	100		2-12%[ea]							Lakes	>66, <520	16-28	*	AC	180[da]		[da]	Schneider 1992
7-12 TL	352		9%[dy]							Ponds	>66, <520	0-4	*	AC	180[da]		[da]	Schneider 1992
$\bar{x}$ = 11 TL	55, 14[fe]		0%		0%	0%	0%	0%		Lakes	122-789		*	PDC	30, 60, 120		Expo?	Bardygula-Nonn et al. 1995
Lepomis macrochirus, bluegill																		
8-10	525	[dc]	1-19%[dd]				3-7%[dd]			Hatch. ponds	167		*	AC,115V	60			Spencer 1967a & b
8-10	525	[dc]	1-58%[dd]				9-16%[dd]			Hatch. ponds	167		*	AC,230V	180[da]		[da]	Spencer 1967a & b
8-10	1200		0-75%[cz]							Hatch. ponds	167		*	AC.230V	180[da]		[da]	Spencer 1967b
8-10	25		4%[db]							Hatch. ponds	100		*	AC,230V	180[da]		[da]	Spencer 1967b
8-10	25		18%[db]							Hatch. ponds	200		*	AC,230V	180[da]		[da]	Spencer 1967b
8-10	25		24%[db]							Hatch. ponds	250		*	AC,230V	180[da]		[da]	Spencer 1967b
8-10	25		40%[db]							Hatch. ponds	333		*	AC,230V	180[da]		[da]	Spencer 1967b
8-10	25		54%[db]							Hatch. ponds	500		*	AC,230V	180[da]		[da]	Spencer 1967b
8-10	25		56%[db]							Hatch. ponds	1000		*	AC,230V	180[da]		[da]	Spencer 1967b
5-18 TL	44		0-0%[dx]							Lakes	>66, <520	13-18	*	AC	180[da]		[da]	Schneider 1992
5-20 TL	102		2-2%[db]							Lakes	>66, <520	22-26	*	AC	180[da]		[da]	Schneider 1992
7-12 TL	166		1%[dy]							Ponds	>66, <520	0-4	*	AC	180[da]		[da]	Schneider 1992

Appendix B. Continued.

Species		Adverse Effects								Environment			Electric Field and Current					Source
			Mortality		Spinal Injuries													
						Spine/Vertebrae												
Lengths (cm) or develop. intervals	No. obs.	Delayed equil., recov.	Short-term	Long-term	Brands	Extern.	Intern.	Intern. hemor.	Other injuries	Where fish were subjected to electric field	Conductivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Frequency (Hz)	Pulse duration (ms)	Waveform	(pc = pers. commun.) (um = unpubl. ms.)
8-10	525	[dc]	1-29%[dd]				0-3%[dd]			Hatch. ponds	167		*	DC,115V				Spencer 1967a & b
9-17		[aw]	0-55%[aw]							Test tank	154	10	=	PDC	1.6			Whaley et al. 1978
9-17		[aw]	0-77%[aw]							Test tank	154	10	=	PDC	8.8			Whaley et al. 1978
9-17		[aw]	0-94%[aw]							Test tank	154	10	=	PDC	16			Whaley et al. 1978
$\bar{x}$ = 13 TL	568, 142[fe]		5%		≥5%	0%	≥1[fe] 0%	≥5%[fe] 0%		Lakes	122-789		*	PDC	30,60, 120		Expo?	Bardygula-Nonn et al. 1995
$\bar{x}$ = 15 TL	5		0%				0%			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
15 TL	1		0				1			Reservoir			*	PDC	80		Sq.?	Zeigenfuss 1995
Micropterus spp., black basses																		
	[c]				0	0	0?			Rivers etc. CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
Micropterus dolomieu, smallmouth bass																		
$\bar{x}$ = 21 TL	145, 29[fe]		1		≥4% 14%	0%	0%[fe]	≥4% 14%[fe]		Lakes	122-789		*	PDC	30,60, 120		Expo?	Bardygula-Nonn et al. 1995
Micropterus salmoides, largemouth bass																		
13-25	100/70		~0%[dg]				0%[dd]			Hatch. ponds	167		*	AC,230V	180[da]		[da]	Spencer 1967a & b
	30		~0%[cc]							Lakes	>66, <520		*	AC	180[da]		[da]	Schneider 1992
$\bar{x}$ = 21 TL	454, 114[fe]		1%		1	0%	1%[fe]	≥1% 2%[fe]		Lakes	122-789		*	PDC	30, 60, 120		Expo?	Bardygula-Nonn et al. 1995
$\bar{x}$ = 17 TL	13		0%				8%			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
$\bar{x}$ = 24 TL	3		0%				0%			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
$\bar{x}$ = 32 TL	4		0%				0%			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
≥20 TL	100's		0%		few					Reservoirs			*	PDC[fv]	~62,73	3.5,8.7	Sq.	Hill & Willis 1994
$\bar{x}$ = 34 TL	6		0%				33%			Reservoir			*	PDC	80		Sq.?	Zeigenfuss 1995
Pomoxis annularis, white crappie																		
15 TL	1		0				0			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
$\bar{x}$ = 15 TL	3		0%				0%			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
19 TL	1		0				0			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
18 TL	1		0				0			Reservoir			*	PDC	80		Sq.?	Zeigenfuss 1995
Pomoxis nigromaculatus, black crappie																		
16 TL	1		0				0			Reservoir			*	PDC	80		Sq.?	Zeigenfuss 1995
Percidae																		
Etheostoma flabellare, fantail darter																		
2.5-7.5		[aw]	0-69%[aw]							Test tank	154	10	=	PDC	1.6			Whaley et al. 1978
2.5-7.5		[aw]	0-76%[aw]							Test tank	154	10	=	PDC	8.8			Whaley et al. 1978
2.5-7.5		[aw]	0-95%[aw]							Test tank	154	10	=	PDC	16			Whaley et al. 1978
Perca flavescens, yellow perch																		
5-10 TL	40		0-0%[ed]						X[ed]	Lakes	>66, <520	10-15	*	AC	180[da]		[da]	Schneider 1992
8-13 TL	66		0-0%[ee]						X[ee]	Lakes	>66, <520	6-8	*	AC	180[da]		[da]	Schneider 1992
10-27 TL	52		0-9%[ef]							Lakes	>66, <520	7-13	*	AC	180[da]		[da]	Schneider 1992

Appendix B. Continued.

Species		Adverse Effects								Environment				Electric Field and Current				Source
Lengths (cm) or develop. intervals	No. obs.	Delay-ed equil., recov.	Mortality		Spinal Injuries				Other injuries	Where fish were subjected to electric field	Conduc-tivity (μS/cm)	Temp. (°C)	Fd tp	Current type	Freq-uency (Hz)	Pulse dura-tion (ms)	Wave-form	(pc = pers. commun.) (um = unpubl. ms.)
			Short-term	Long-term	Brands	Spine/Vertebrae Extern.	Spine/Vertebrae Intern.	Intern. hemor.										
9-19 TL	16		94% [cd]							Lakes	>66, <520	19-27	*	AC	180[da]		[da]	Schneider 1992
20 TL	1		0				1			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
x̄ = 25 TL	11		0%				0%			Reservoir			*	PDC	80		Sq.?	Zeigenfuss 1995
Stizostedion vitreum, walleye																		
	13		~0%[cc]							Lakes	>66, <520		*	AC	180[da]		[da]	Schneider 1992
33-44 TL	5						40%			Lakes			*	PDC?				Newman um 1991
19-48 TL	12						25%			Rivers	17,800?[cs]	26	*	PDC	30			Newman um 1991
	[c]				0	0	0?			Rivers etc,CRB	<50->5000	>0->30	*	PDC	60			Krueger pc
33? TL	1						0	0		Rivers	600	11	*	PDC	60	8?	Sq.	Fredenberg 1992
x̄ = 42 TL	6		0%				17%			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
x̄ = 20 TL	24		0%				21%			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
x̄ = 21 TL	2		0				0			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
40 TL	1		0				0			Reservoir			*	PDC	80		Sq.?	Zeigenfuss 1995
18-43 TL	13						31%			Lakes	15,300?[cs]	22	*	PDC	120			Newman um 1991
Stizostedion canadense, sauger																		
≥47 TL	20						0%	0%		Rivers	~500	7	*	PDC	60	8?	Sq.	Fredenberg 1992
32-53 TL	6						0%	0%		Rivers	600	11	*	CPS	240/15	2.6/11	Sq.	Fredenberg 1992
Sciaenidae *Aplodinotus grunniens*, freshwater drum																		
30-43 TL	7		0%		0%		0%	0%		Rivers	351-425	12-15	*	PDC[fs]	40	6.3	Sq.	Grisak 1996
x̄ = 32 TL	2		0				0			Reservoir			*	PDC	60		Sq.?	Zeigenfuss 1995
General (unspecified families or species)																		
		X[ay]			X					Rivers, reserv.			*	all				Beyers pc
Juv-ad [bd]							0 [bc]			Rivers etc, CRB	250-3500		*	PDC,DC				Burdick pc
			>0.1%[az]							Rivers, streams	<100		*	PDC				Gowan pc
[bb]			0?			0				Rivers, CRB			*	PDC				Kinsolving pc
[bc]			~0.01%		0					Rivers, CRB	300-2000	5-25	*	PDC				Valdez pc
4-96		X	[ba]		X					Rivers etc, CRB			*	PDC				Trammell pc
4-96		X	[ba]		X					Rivers etc, CRB			*	CPS	240/15	2.6/11	Sq.	Trammell pc

Footnotes:

[a]Abbreviations in and comments on table headings: Develop. = Developmental; No. Obs. = number of fish observed (i.e., examined, X rayed, or necropsied); Delayed Equil., Recov. = delayed equilibrium or recovery; Short-term mortality is immediate to several days; Brands are sometimes referred to as burns or bruises and usually indicate spinal damage; Extern. = external signs of spinal damage other than brands (e.g., bent back); Intern. = internal observations of damage to the spine or vertebrae based on X-ray analysis or necropsy (regardless of severity rating); Intern. Hemor. = internal hemorrhages observed along or in tissues around the spine during necropsy (regardless of severity rating); μS/cm = microsiemens per centimeter; Temp. = temperature; °C = degrees Celsius; Fd tp = field type (heterogeneous or homogeneous); Hz = hertz; ms = milliseconds; pc = personal communication; um = unpublished manuscript.

Appendix B. Continued.

Footnotes (continued)

[b]Abbreviations in body of table: TL = total length; FL = fork length; juv. = juveniles; ad. = adults; yoy = young-of-the-year juveniles; X = one or more observations but quantity not specified; "~" = approximately; "<" = less than; ">" = greater than; Lab. = laboratory; CRB = Colorado River Basin; reserv. = reservoirs; Hatch. = hatchery; Exp. = experimental; "*" = heterogeneous field (voltage gradient diminishes with distance from electrodes); "=" = homogeneous field (voltage gradient constant); AC = alternating current; DC = (continuous) direct current; PDC = pulsed direct current; CPS = trademark for a specific pulse train by Coffelt Manufacturing, Inc. (complex pulse system–trains of three 1.6-ms, 240-Hz pulses at 15 Hz); Sq. = square; Expo. = exponential; ¼ Sine = quarter sine; ½ Sine = half sine (rectified AC); pc = personal communication; um = unpublished manuscript.

[c]Mortalities due to notochords that were "completely blown apart."

[d]Specimens were subjected to 2 to 4 5-s electric field exposures within a 6-week period, at least 7-d apart; they were acclimated to test conductivities 2.5-7 d prior to the test and observed for 3 d after exposure.

[e]Fish were captured and filleted for contaminants analyses.

[f]Only injury was considered a freak accident–specimen was trapped between a plate cathode and the boat.

[g]Hemorrhaging (brands?) seemed proportionately greater in Grand Canyon electrofishing using CPS system than in Upper Colorado River Basin using a more typical PDC.

[h]Only 1 injury was observed, a brand on a specimen suspected to have touched the cable anode; it and fish knocked out completely and floating on surface recovered slowly but all seemed fine on release. Specimens that were subsequently recaptured or followed after radiotagging appeared normal.

[i]Twenty fish were captured by electrofishing, radiotagged, and followed for 4 months (except one that subsequently died of unknown causes).

[j]Large Colorado pikeminnow which contacted the anode bled at the gills and "everything"; a 112 mm specimen that was captured belly-up with gills still going and no obvious bleeding died (viscera were removed for study and the remainder of the fish was preserved).

[k]Large female with bruise (might be same fish reported by McAda pc[h]); single and multiple recaptures appeared normal.

[l]Brands usually observed in caudal region.

[m]Twenty fish were captured by electrofishing, radiotagged, and followed for 4 months (except two that were lost).

[n]No visible external injuries or high mortality observed, but fish were typically "knocked out cold" and floated slowly to the water surface.

[o]Most were completely tetanized, "stiff as boards," and floated to the surface behind the boat.

[p]Injuries from electrofishing in previous years–back half of fish stopped growing and the fish started to look like footballs.

[q]Several unspecified injuries among salmonids; necropsied fish same as those reported by Krueger pc.

[r]No immediate mortality; short-term mortality among seined controls was higher (12%), but most mortality among electrofished specimens occurred on day 1 of the 7-d holding period whereas most seining mortalities (controls) occurred on day 7.

[s]Spinal injury was higher (9%) and sometimes more severe among seined controls. Hemorrhage was nearly the same for seined controls (5%). None of the injuries observed among electrofished specimens were considered new electrofishing injuries because hemorrhages were not observed in association with specific vertebral damage and injuries appeared as great or greater among seined controls. However, hemorrhages may have cleared up during the 7-d holding period.

[t]Of the short-term mortalities, 10% were immediate; mortalities among seined controls, immediate and after 7 d, were as great or greater (8% and 42%); mortalities for controls occurred throughout the 7-d holding period, whereas most mortalities for electrofished specimens occurred during the first day.

[u]Spinal injuries, internal hemorrhages, and external hemorrhages were as great or greater among seined controls (2%, 19%, and 42%). No spinal injuries were considered new electrofishing injuries.

[v]Brands were hemorrhages immediately below and posterior to the dorsal fin and were observed on young-of-the-year as well as older fish.

[w]Yellowstone cutthroat trout.

[x]High percentage of fish recaptured 1 and 2 years later.

[y]*Oncorhynchus mykiss* taken within 0.5 m of the electrode seemed likely to be injured.

[z]Numbers of fish observed for: short-term mortality and bruises/spinal damage and hemorrhages.

[aa]Of mortalities during the 4-d holding period, 4% were immediate.

[ab]Vertebral damage and hemorrhage data was based on the 10 mortalities and 22 of the survivors > 40 cm FL; of fish over 40 cm in length, 41% of the survivors suffered major spinal injury and 53% suffered either major spinal injury or death.

[ac]Spinal injury was posterior to dorsal fin; based on external examination only.

[ad]Fish were frozen, X-rayed, and necropsied; those found to have spinal injuries also had associated internal hemorrhages and splintered bones from compression fractures. Twelve hatchery specimens were used as non-electrofished controls.

[ae]Fish were held perpendicular to the lines of current in a plastic cage.

[af]Fish were held parallel to the lines of current in a plastic cage.

[ag]Negligible, only one mortality in a whole series of tests. Indices of fatigue, 20-240 s (mostly under 60 or 120 s), varied with electrofishing equipment, increased with field intensity and fish length, and decreased with successive exposures.

[ah]Brands noted on larger specimens.

[ai]No immediate mortality, but all deaths occurred within the first 4 hr.

[aj]Brands disappeared by the end of the 7-d holding period; all branded specimens had associated spinal injuries.

[ak]Based on presence of both vertebral damage and hemorrhage in the same location, 17% (21% including mortalities) of the fish determined to have new electrofishing injuries; however, after a 7-d holding period, most hemorrhages may have already dissipated. Fish collected by hook & line (N=11) experienced no mortality, 18% vertebral damage, and no hemorrhages.

[al]All short-term mortality was immediate; fish were not held beyond normal processing.

[am]Seven fish with spinal injuries had associated brands.

Appendix B. Continued.

Footnotes (continued)

[an]Hemorrhages were observed at the same location as vertebral damage in 18% of the fish. Beach seine and hook and line collections yielded 2% immediate mortality, 5% with vertebral damage; and 13% with internal hemorrhages.
[ao]Long-term mortality was not significantly different from that for other gear based on year-after recapture rates in a river and a lake. Growth rates for fish 30 cm and greater were not significantly different for fish after one year in the lake; data was insufficient to determine significance of growth differences for smaller fish and for those from a river.
[ap]Short-term, 7-d mortality was lower than for fish collected by other gear (6%); none was immediate.
[aq]Some spinal injuries and hemorrhages were greater (12% and 10% respectively) among fish collected by beach seine or hook and line. Regardless of gear, vertebral damage and hemorrhages were not observed in the same locations; however, hemorrhages may have begun to clear up prior to specimen analysis.
[ar]Mortalities within one month holding period among electrofished (n=140) and control (n=70) specimens were nearly identical at 8% and 9%, respectively (5% of shocked injured fish and 9% of shocked uninjured fish)–no differences (death of all fish in one of five holding ponds was considered an accident and specimens were not included in analysis). N=172 for fish originally shocked and examined for spinal injury.
[as]Short-term mortality was immediate (no fish were held); mortality for controls was greater (2% for hook and line, 1% for gill nets, and 23% for trap nets) than for electrofished specimens.
[at]Long-term recapture rates were 9% for controls and 5% for electrofishing. Long-term growth was not significantly different.
[au]Incidence of vertebral damage and hemorrhages was 1% and 3%, respectively, for fish taken by hook and line, fyke trap, and gill nets. Based on presence of both vertebral damage and hemorrhages at the same location, 13% of electrofished specimens were considered to have new electrofishing injuries.
[av]All fish with hemorrhages also had obvious and severe vertebral damage.
[aw]Mortality increased progressively with duration of exposure and pulse rate; mortality ranged from low or negligible at or below 15 s and even 30 s at very low frequency (1.6 Hz) to 95% at 180 s and 16 Hz). Recovery time also increased with length of exposure. Fish were held parallel to the lines of current.
[ax]Electrofished sculpins commonly flared their gills and often died.
[ay]Some fish required 5-10 minutes for recovery of equilibrium.
[az]More than 5000 fish held overnight in baskets to assess mortality; most were salmonids under 18 inches.
[ba]Never observed death due to obvious injuries.
[bb]Fish in general, except as noted above for *Cyprinus carpio* and *Oncorhynchus mykiss* by Kinsolving pc.
[bc]Fish other than species listed above by Valdez pc.
[bd]Fish other than Upper Colorado River Basin salmonids and endangered species listed above by Burdick pc.
[be]Necropsied fish same as those reported by Krueger pc.
[bf]Brood stock: a 20-pound female and 2 to 5-pound males. Eggs fertilized well and survival was high.
[bg]Duty cycle.
[bh]Delayed mortality during 35-d holding period might have been short-term rather than long-term but no immediate mortality and delayed mortality was less than for controls (5%) or fish subjected to fly fishing (5% initial and 3% delayed). The authors specifically noted that brands resulted from internal hemorrhages and possible breakage of the vertebral column. Stamina based on a swimming performance index the day after treatment was significantly lower for electrofished than control or fly-fished specimens.
[bi]No immediate mortality. Mortality for yearling juveniles over 1.4 yr was similar to controls (7% versus 8% for controls). Survival and growth to spawning, fecundity, and survival of offspring (eggs and larvae) were similar for both exposed and control fish. Voltage gradient was 0.75 V/cm, exposure was 30 s, and 4-84% of the fish were narcotized by the current. Waveform pulses were described as having an exponential leading edge and a square trailing edge (square waveform with a leading edge spike?).
[bj]No immediate mortality. Data for the first 4 months were not properly recorded and are unknown (< 10%); the number of exposed fish were reduced to 856 at that point and from the 4th month to 2.5 yr after exposure, mortality was less than for controls (10% versus 16% for controls with numbers of exposed fish again reduced to 236 for the last half year of observations). Survival and growth to spawning, fecundity, and survival of offspring (eggs and larvae) were similar for both exposed and control fish. Voltage gradient was 1.0 V/cm, exposure was 30 s, but none of the yoy were narcotized. Waveform pulses were described as having an exponential leading edge and a square trailing edge (square waveform with a leading edge spike?).
[bk]Similar X-rays of 104 gill-net-caught, fish-trap-caught, and hatchery *Oncorhynchus mykiss* revealed no vertebral damage; similar necropsy of 16 gill-net-caught and 50 fish-trap-caught *Oncorhynchus mykiss* revealed 13% and 4% with spinal-region hemorrhages, respectively, but all were minor (class 1 by Reynold's um 1992 classification).
[bl]30% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both.
[bm]18% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both.
[bn]According to Fredenberg's (1992) note on page 8 of his text, current was suspected to be PDC rather than DC as originally recorded and reported in Fredenberg's Appendix B data.
[bo]98% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both; sample was a mixture of 35 *Oncorhynchus mykiss* and 7 *Oncorhynchus clarki*.
[bp]78% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both.
[bq]Sample was a mixture of 9 *Oncorhynchus mykiss* and 3 *Oncorhynchus clarki*.
[br]55% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both.
[bs]31% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both.
[bt]73% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both.
[bu]90% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both; sample was a mixture of 31 *Oncorhynchus mykiss* and 8 *Oncorhynchus clarki*.
[bv]65% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both.

Appendix B. Continued.

Footnotes (continued)

[bw]64% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both; hybrid current with PDC above half-voltage DC (referred to as a half-pulse waveform by Fredenberg 1992).

[bx]All branded fish (N = 39) were X-rayed, necropsied, and found to have spinal injuries, 64% of which were classified as moderate to severe; among unbranded fish (N=113), 50% suffered vertebral damage or (and) spinal-region hemorrhages, 30% of which were classified as moderate to severe; fish were collected from the same river using DC and PDC (60-Hz square and CPS).

[by]10% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both.

[bz]Hybrid current with PDC above half-voltage DC (referred to as a half-pulse waveform by Fredenberg 1992 and Dalbey et al. 1996).

[ca]44% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both.

[cb]62% injured overall, i.e., specimens with only vertebral damage revealed by X-rays, only spinal-region hemorrhages revealed by necropsy, and both.

[cc]Initially, 150 fish were retained for post-electrofishing observation, but only 88 fish were recovered 7 d later due to holes in the in-river pen net.; of these 4 *Oncorhynchus mykiss* and 1 *Salmo trutta* died. None of the deaths were immediate. 50 *Oncorhynchus mykiss* and 28 *Salmo trutta* were examined by X ray and necropsy.

[cd]Characteristics of the PDC current used were uncertain due to a control box that was found to be "seriously out of calibration."

[ce]Also reported by Wyoming Game and Fish Department 1990.

[cf]Deaths for fish taken by 60-Hz PDC occurred in the hatchery truck during transit and were probably due to stresses in addition to electrofishing (any occurrences of immediate mortality were not reported); output voltage 280-300V.

[cg]No immediate mortality.

[ch]Fish from stream segment electrofished with 4 passes.

[ci]Fish from stream segment electrofished with only 1 pass.

[cj]Also reported by Meyer and Miller 1991 (abstract) and um 1991; output voltage for 40-Hz PDC 370-390V, possibly 1/4 Sine based on Meyer and Miller (1990), for CPS, 460-470V.

[ck]Combined mortality for fish subjected to DC, PDC, and CPS during a 203 d holding period in a hatchery; most deaths occurred in the first 30 d (factors other than or in addition to electric currents may have been responsible).

[cl]Number captured and examined for brands after first exposure (two passes through 5-m wide raceways) / number captured by a second electrofishing effort (again two passes) 7 d later and necropsied for spinal hemorrhages or anomalies later; controls showed no signs of spinal hemorrhages or anomalies. Mortalities were for 7 d period after first exposure, N =~30 fish per trial.

[cm]Brand data from McMichael and Olson (um 1991), also mentioned in McMichael et al. 1991 (abstract); duty cycle 13% for PDCs (McMichael pc) and waveform square (Johnson pc).

[cn]Account covers and is recorded here under both *Oncorhynchus mykiss* and *Salmo trutta*.

[co]Walk electrofishing using Coffelt VVP-2C, assumed to output 60-Hz, ½-sine PDC.

[cp]Boat electrofishing using Coffelt VVP-2C, assumed to output 60-Hz, ½-sine PDC.

[cq]Overall size range for fish collected from all four streams by all methods in study; size range for specific stream not reported; however, incidence of injuries overall for three size groups are given as separate entries in this table.

[cr]Among 46 fish captured by angling from stream with a conductivity of 440 μS/cm, 12% were determined to have vertebral injuries (but no hemorrhages); however, no vertebral injuries or hemorrhages were found in 39 specimens angled from the other study streams which had conductivities ranging from 43 to 64 μS/cm. Percentages of fish with either spinal injuries or hemorrhages among all four streams ranged from 14% to 41% using AC and 9 to 41% using PDC.

[cs]Reported conductivity or units seem unlikely–17.8 mS/cm for the river and 15.3 mS/cm for the lake.

[ct]Fish were held for 10 d and mortality was delayed; comparable mortality for fish captured by seining (N=16) and angling to exhaustion (N=16) was 6% and 87% respectively.

[cu]Based on X rays, 4% of the fish were found to have vertebral anomalies before exposure to the electric current with no change afterward.

[cv]Other injuries noted included hemorrhaging from the gills or vent, hemorrhaging in the skin around the vent, dilated and clotted blood vessels in the region of the brain, intestine protruding from the vent, and persistent paralysis suggesting injury to the nervous system.

[cw]Most of these mortalities were immediate (mostly fish that escaped the scap net and suffered extensive exposure to the current); no mortalities occurred among controls. Fish were exposed to the current at the beginning, middle, and end of a 6-wk holding period by holding them in the field with a scap net for 15 s about 30 cm from an electrode (positive electrode in DC).

[cx]All mortalities were delayed; no mortalities occurred among a similar number of controls. Fish were exposed to the current at the beginning, middle, and end of a 6-wk holding period by holding them in the field with a scap net for 15 s about 30 cm from an electrode (positive electrode in DC).

[cy]Immediate mortality; immediate mortality among controls (N=403) was 2%. Comparing treatments, square rather than half-sine waveforms, higher frequencies (30 vs. 15 Hz) and higher water conductivities (67 & 100 vs. 200 & 1000 μS/cm) resulted in higher mortality. Fish were forced through an electrical array of 5 rows of electrodes with a cyclic pattern of positive-negative electrode configurations that changed with every pulse. Fish were held for 30 d; except for frequency, patterns of differences among treatments for delayed mortality (generally between 7% and 18%) were similar to those for immediate mortality but not significantly different from controls.

[cz]Mortality was highly correlated with exposure times from 1% at 1 s (0% at 4 s) to 75% at 300 s; for exposures ≥60 s, most mortalities were immediate, occurring during the first 5 min. of the 24 h holding period; for lesser exposures, most mortalities were delayed but occurred within the first 2 h.

[da]3-phase, 230V AC; 3 sine waveforms phase shifted by a third.

[db]Exposure time was 60 s; most mortality occurred in the first 2 h and generally a third to a half was immediate.

[dc]Recovery time for survivors increased with exposure time (and was greater for 230-V, 180-Hz, 3-phase AC than 115-V, 60-Hz, single-phase AC).

[dd]Exposure times varied from 1 to 120 s; mortality increased with exposure time but did not correlate well with incidence of injury; incidence of injury was independent of exposure time; most mortality occurred during the first 2 h of the 24 h holding period.

[de]Fish held parallel to a field of 6 V/cm for 60 s.

Appendix B. Continued.

Footnotes (continued)

[df]Fish held perpendicular to a field of 6 V/cm for 60 s.

[dg]N = 100 for mortality; N = 70 for spinal injuries. Exposure was varied from 1-300 s and fish were held for 24 h. Only one mortality was recorded (60 s, delayed) and this was believed to be due to handling rather than the electric current.

[dh]Three or four passes; 15 d holding period; immediate mortality less than 1%; no mortality among controls. Data combined for burns and other external signs of spinal injury (erratic swimming) based on both *Oncorhynchus mykiss* and *Salvelinus fontinalis*; no external signs of injury observed among controls.

[di]2.5% of all 2250 *Oncorhynchus mykiss* and *Salvelinus fontinalis* examined are estimated to experienced spinal injury (6 of 28 dead, 27 of 36 abnormal, and 23 of 2186 normal fish, latter extrapolated from observation of one injury among 96 normal fish examined); no injured vertebrae among controls.

[dj]Mortality not significantly different from similar numbers of kick-seine "controls" (0-12% for fish collected in late winter at 5-8°C; 0-14% for fish collected in early summer at 14-16°C); single exposure at 600V; 30 d holding period.

[dk]Mortality not significantly different from similar numbers of repeatedly handled kick-seine "controls" (45-50%); probably most affected by repeated handling; multiple exposures, once per week for a month at 600V; monitored between treatments.

[dl]Little or no mortality during 30 d observation period.

[dm]Mortality increased with exposure time (0.5-20 min) and voltage gradient (1, 2, and 4 V/cm).

[dn]Mortality increased with exposure time (2-10 min) and less consistently with water conductivity (and thereby current density); voltage gradient was constant at 2 V/cm.

[do]Immediate mortality (1 h observation period), 30 s exposure; mortality increased with voltage gradient from the low value at 3-4 V/cm to the high value at 15 V/cm; no size effect; mortality among 2800 controls was 0.5%.

[dp]Immediate mortality (1 h observation period), 30 s exposure at a constant 4 V/cm.; mortality increased with water conductivity (and therefore current density); at higher conductivities, mortality tends to be greater at higher temperatures. No consistent size effect; mortality among 2800 controls was 0.5%.

[dq]Voltage gradient constant at 4 V/cm; mortality increased with exposure time and temperature (values at 14°C tend to be less than at 18°C); also tends to increase with size.

[dr]Voltage gradient held constant at 2V/cm; mortality increased with exposure time (3-10 min for trials at 2 Hz and 0.5-3 min for 8 Hz) but occurred at shorter exposures times for 8 Hz than for 2 Hz (cumulative current on time 4 times greater at 8 Hz).

[ds]Voltage gradient held constant at 2V/cm; mortality increased with exposure time (0.5-3.0 min) but tended to be higher for the shorter pulse duration (20 ms versus 80 ms).

[dt]Voltage gradient held constant at 4V/cm, 30 s exposures; mortality tended to increase with pulse rate and specimen size, but results could be confounded by variable conductivities.

[du]N = number exposed/ number necropsied. 80 fish exposed for 5 s, 80 for 10 s, and 80 for 20 s, then held 13 d for observation; mortality similar among 80 controls suggesting no effect by electrofishing. Necropsy of 3 electrofished and 1 control fish that had died during the holding period revealed no signs of spinal injury.

[dv]25 fish exposed for 5 s, 25 for 10 s, and 25 for 15 s; mortality among controls was also 0%.

[dw]Fish were subjected to 1 min at 0.5 V/cm to initiate narcosis then held in narcosis at 0.25 V/cm for 1, 2, 4, or 6 h, (N=15 plus 15 controls each), then held for 25 d; all mortalities (2) occurred in fish narcotized for 6 h; fish narcotized for 1 or 2 h recovered instantaneously whereas those narcotized for 4 or 6 h had difficulty resuming swimming activity for up to 12 h. Photonegative behavior and growth during the holding period did not differ from that of controls.

[dx]Held for 1 d in cages in the lake.

[dy]Held for 10 d in pond; some mortalities were probably due to the stress of handling and incomplete recovery of all fish upon draw-down of the pond rather than electrofishing itself.

[dz]Held for 1-4 d in cages in the lake.

[ea]Held for 22 d in cages in the lake.

[eb]Held for 31 d in cages in the lake.

[ec]Based on comparable recapture rates 1 to 2 yr after initial capture by electrofishing, trap net, and angling (largemouth bass only); growth also appeared to be unaffected by capture method (although angled *Micropterus salmoides* were notably younger and larger upon capture and had grown most between initial capture and recapture.

[ed]Held for 3 d in cages in the lake; half of the fish (20) held were selected from among fish with obvious aggregations of blood in the sinus venosus near the base of the gills, the other half were selected from those without such an aggregation of blood; The aggregations of blood dissipated within 1 d and the fish seemed otherwise normal.

[ee]Held for 10 d in cages in the lake; half of the fish held (33) were selected from among fish with obvious aggregations of blood in the sinus venosus near the base of the gills, the other half were selected from those without such an aggregation of blood; The aggregations of blood dissipated within 1 d and the fish seemed otherwise normal.

[ef]Held for 30-38 d in cages in the lake.

[eg]Held for 40 d in cages in the lake; mortality likely due to stress of handling, confinement, low food, and high temperatures rather than electrofishing.

[eh]Species assumed to be *Salmo trutta*. 10 fish held in net 50 cm from positive electrode (lower mortality value) and 10 held 20 cm from positive electrode (higher mortality value); fish exposed for 20 seconds initially facing positive electrode; all mortality assumed to be immediate.

[ei]Rippled DC, generated by smoothing half-wave, rectified AC.

[ej]50% duty cycle but frequency not reported.

[ek]33% duty cycle but frequency not reported.

[el]400 V.

[em]400 V; full-wave rectified AC.

[en]62-145 V (up to 180 V?) for 5-30 s; recovery delayed in some fish to beyond a minute at higher energy densities (125 and 188 millijoules/cm^3); longer fish, especially those about 80 mm TL or longer required longer recovery times; fish requiring more than 2 minutes recovery time frequently died.

Appendix B. Continuued.

Footnotes (continued)

[co]High incidence of bleeding at the gills observed by Montana biologists regardless of current–"literally dozens of mountain whitefish come to the electrode under taxis with blood streaming in the water."

[cp]20 fish were treated and frozen, for x-ray analysis and if such indicated possible spinal injury, fish were necropsied; likewise for 20 of 50 treated and reared for 35 d, and 20 controls reared for 35 d. four of the treated and reared fish died within 24 h and were added to the frozen batch, bringing the number of treated fish examined to 44. There was no indication of spinal trauma.

[cq]Current was generated by a Coffelt BP-6 backpack electrofisher generating a half-rectified waveform (half-sine wave pulses?); output was measured at 0.6 A, 365 V peak, 93 V mean; mean voltage gradient in the homogeneous field was 0.9-1.0 V/cm ; fish were exposed for 10 s.

[cr]Mortality within first 7 d. For DC, no immediate mortality and most of the 12 mortalities may have resulted from increased stress due to recapture following escape from a raceway prior to release in a storage pond. For hybrid PDC-DC (half pulse) current, two specimens died, one prior to release in a storage pond for monitoring subsequent survival and growth. For PDC, one specimen died within 7 d.

[cs]Fish were held in a raceway for 182 d for each of the six treatment currents; there was no significant difference among the waveforms despite a mortality range from 0% for DC to 25% for 20 and 30-Hz PDC, probably because of small sample size. Mortality among controls held 203 d was 10%.

[ct]Of 102 shocked for 5 s at a mean of 2.3 V/cm and 50 control fish held for 203 d, 52% of the shocked and injured fish, 29% of the shocked and uninjured fish, and 10% of the control fish died. However, the difference between shocked injured and shocked-uninjured fish was not statistically significant, nor were any length differences among these groups and controls. Most injuries were class 2. 83% of overall mortality occurred within the first 30 d with no significant difference over time between shocked-injured, shocked-uninjured, and controls.

[cu]Boat electrofishing, mobile (throwable) anode, peak 2.3 V/cm at 15 cm from anode; sixteen brown trout not evaluated for spinal injuries due to poor x-rays. Data also from Thompson (1995).

[cv]Boat electrofishing, mobile (throwable) anode, peak 7.4 V/cm at 15 cm from anode. Data also from Thompson (1995).

[cw]Boat electrofishing, mobile (throwable) anode, peak 3.4 V/cm at 15 cm from anode; six rainbow trout not evaluated for spinal injuries due to poor x-rays. Data also from Thompson (1995).

[cx]Shore-based wade electrofishing, multiple mobile anodes, peak 0.5 V/cm at 15 cm from anode; eight brown trout not evaluated for spinal injuries due to poor x-rays. Data also from Thompson (1995).

[cy]Shore-based wade electrofishing, multiple mobile anodes, peak 1.2 V/cm at 15 cm from anode; sixteen brown trout not evaluated for spinal injuries due to poor x-rays. Data also from Thompson (1995).

[cz]Shore-based wade electrofishing, multiple mobile anodes, peak 1.1 V/cm at 15 cm from anode; two rainbow trout not evaluated for spinal injuries due to poor x-rays. Data also from Thompson (1995).

[fa]Percentage mortality based on 773 fish, 145 s-rays were unreadable; no injuries observed among a subsample of 20 controls; (peak?) voltage gradient was 1.6 V/cm in 60 cm x 30 cm x 30 cm tank.

[fb]Percentage mortality based on 1134 fish, subsample of 184 fish x-rayed; no injuries observed among a subsample of 20 controls; (peak?) voltage gradient was 3.2 V/cm.

[fc]Subsample of 10 fish x-rayed and necropsied. Short-term mortalities include 3 fish that died within 24 h and 6 more that died within 7 d. Data represents handled and unhandled shocked fish from three-pass depletion sampling at three consecutive stations.

[fd]Subsample of 54 fish x-rayed and necropsied. Short-term mortalities include 4 fish that died within 24 h and 7 more that died within 7 d. Data represents handled and unhandled shocked fish from three-pass depletion sampling at three consecutive stations.

[fe]Number of observations for short-term, 3-d, mortality; all dead fish had soft tissue damage with internal hemorrhaging from damaged dorsal aorta and other vessels in region of the caudal peduncle, and in *L. macrochirus* from below mid-dorsal fin area. Spinal injuries were subluxations (partial separation of vertebrae) or misalignments.

[ff]Fish taken during three-pass depletion electrofishing in three successive years from a stretch of stream sampled in prior years by electrofishing; externally evident injuries (mostly representing healed injuries from previous years) progressively (cumulatively) increased during those years for all salmonids, but greatest in year two and least in year 3 for longnose sucker..

[fg]Fish taken during single-pass electrofishing in three successive years from a "control" stretch of stream not previously sampled by electrofishing; externally evident injuries (mostly representing healed injuries from previous years) were absent in first year.

[fh]Healed injuries among brook, brown, and rainbow trout found dead (N=48),that died after electrofishing and handling (N=62), or were purposely sacrificed to assess difference between number of fish with externally detected injuries (mostly healed old injuries) and number of healed injuries detected by dorsal and lateral x-rays. 153 x-rays were taken, but only 114 of those that were readable were of fish without externally obvious injuries.

[fi]PDC frequency and duty cycle (50%) assumed same as for Kocovsky et al. (1997).

[fj]For each current (AC-sine, AC-triangular, PDC-36% duty cycle with unreported waveform; all 50-Hz), individual fish were exposed for 10, 30, or 60 s at 15, 30, 45, 60,75, or 90V (corresponding field intensities were calculated at 0.35, 0.70, 1.1, 1.4, 1.7, and 2.1 V/cm; rms for AC, peak for PDC). All injured with sine AC suffered cutaneous hemorrhages along their entire body length; those with triangular AC had cutaneous hemorrhages in their paired and single fins.

[fk]36% duty cycle, waveform not reported; wild-caught brood stock exposed for 10 s with a peak output of 60V and field intensity of 0.58 V/cm (138 $\mu W/cm^3$ if ambient conductivity 410 $\mu S/cm$).

[fl]Fish subjected to peak field intensity of 1.7 V/cm.

[fm]Fish exposed as groups to peak field intensities of 0.2 to 1.7 V/cm for 3.6 to 100 s.

[fn]No damage was observed externally or to internal organs, however, during 10-s exposures in homogeneous fields with a peak intensity of 1 V/cm, tetany was induced and gametes were expelled from all ripe fish, at least several hundred eggs for each female.

[fo]Preswimup larvae tested using 10 s exposures at 1.2 V/cm peak (also 5 and 10 V/cm for 60-Hz PDC); delayed recovery was just several seconds; no external physical or behavioral anomalies were detected, but subsequent growth was reduced over that of controls during a four-week monitoring period after treatment.

[fp]10 s exposures, 7% at threshold for taxis (0.5 peak-V/cm), 3% at threshold for narcosis (0.7 peak-V/cm), and 20% at threshold for tetany (1.1 peak-V/cm).

[fq]10 s exposures, 7% at threshold for taxis (0.5 peak-V/cm), 10% at threshold for narcosis (0.6 peak-V/cm), and 27% at threshold for tetany (1.0 peak-V/cm).

[fr]10 s exposures, 23% at threshold for taxis (0.4 peak-V/cm), 13% at threshold for narcosis (0.6 peak-V/cm), and 20% at threshold for tetany (1.0 peak-V/cm).

[fs]10 s exposures, 7% at threshold for taxis (0.8 peak-V/cm), 10% at threshold for narcosis (1.0 peak-V/cm), and 7% at threshold for tetany (1.4 peak-V/cm).

[ft]10 s exposures at threshold for tetany (0.8 peak-V/cm).

Appendix B. Concluded.

Footnotes (concluded)

[fu]According to Barton (pc), shocked fish rolled belly up and were motionless but there was no evidence of tetany, after exposure they quickly recovered within a minute or so and showed no signs of external injuries or brands.
[fv]Fish were exposed to electric current for 20 s then, to simulate additional stress of handling, to 0, 1, 2, or 4 min of air.
[fw]Electrical output originally reported as 80-Hz, 50% duty cycle pulsed AC and pulsed DC from Coffelt VVP-15 Electrofisher, but later (Van Zee et al. 1996) corrected to 62-Hz, 3.5-ms, 22%-duty-cycle, square-wave PDC and 73-Hz, 8.7-ms, 64%-duty-cycle, square-wave PDC (ignoring trailing positive spike and small, exponential negative pulse between more normal positive pulses), respectively, as determined by digital oscilloscope tracings.
[fy]Output voltage about 300 V for DC and 400 V of PDC; Effective field (0.1-1.0 V/cm) mapped at up to 1.6 m from the anode, about 4.5 V/cm at 1 cm from the spherical anode with 1.0 V/cm occurring between 20 and 40 cm from the anode; voltage gradient at 1 cm from the boat about 0.11-0.26 V/cm.
[fz]Fish captured by trawl, placed in plastic bucket with holes, and exposed for 10 s to electrical field in the river about 1 m from the anode (about 0.18 V/cm); fish succumbed to tetany but revived within 1 min. Because of size, assessment of injuries may not be conclusive.
[ga]Conductivity calculated from a reported resistivity of 10,000 ohm per inch cube, which, is assumed to equate to 10,000 ohm-in or 25,400 ohm-cm.
[gb]One-minute exposures at 0.5-0.6 V_m/cm (below to just above minimum threshold for stun).
[gc]One-minute exposures at 0.7 V_m/cm.
[gd]One-minute exposure at 0.8 V_m/cm.
[ge]One-minute exposure at 1.0 V_m/cm.
[gf]Five-minute exposures at 0.2-0.5 V_m/cm
[gg]Five-minute exposures at 0.6-0.7 V_m/cm
[gh]Five-minute exposures at 0.8 V_m/cm.
[gi]Field intensity increased gradually from 0 V/cm to threshold for twitch then maintained for 5 s.
[gj]Field intensity increased gradually from 0 V/cm to threshold for taxis then maintained for 5 s.
[gk]Field intensity increased gradually from 0 V/cm to threshold for narcosis then maintained for 5 s.
[gl]Field intensity increased gradually from 0 to 1 V_p/cm, sufficient to ensure tetany, then maintained for 5 s.
[gm]10 s exposure at 1.5 V_p/cm, sufficient for tetany and lowest field intensity for experimental setup using Smith Root GPP 5.0.
[gn]Some individuals required more than 15 min to recover equilibrium.
[go]Electrofishing plus handling mortality usually <25%, but >50% during warm periods; that for all other species collected was always < 11% (taxa unspecified).

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13. ABSTRACT (Maximum 200 words)
Electrofishing, which involves a very dynamic and complex mix of physics, physiology, and behavior, has been a valuable sampling technique for over half a century, but its potentially harmful effects on fish must be recognized, monitored, and avoided or minimized, especially with respect to populations of endangered species. Spinal injuries and associated hemorrhages, although often not externally obvious or fatal, can occur anywhere in the electrofishing field at or above the intensity threshold for twitch. These injuries are believed to result from powerful convulsions of body musculature caused mostly by sudden changes in voltage. Significantly fewer spinal injuries are reported when direct current, low-frequency pulsed direct current (#30 Hz), or specially designed pulse trains are used. Salmoninae are especially susceptible. Endangered cyprinids of the Colorado River Basin are generally much less susceptible, but the endangered catostomid *Xyrauchen texanus* appears sufficiently susceptible to warrant minimal-use policy. Other harmful effects, including bleeding at gills or vent and excessive physiological stress, are also of concern. Mortality, usually by asphyxiation, is a common result of excessive exposure to tetanizing intensities near electrodes or poor handling of captured specimens. Reported effects on reproduction are contradictory, but electrofishing over spawning grounds can harm embryos.

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